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RAPID COMMUNICATION / COMMUNICATION RAPIDE

Base cation reservoirs in soil control the buffering capacity of lakes in forested catchments

Daniel Houle, Rock Ouimet, Suzanne Couture, and Christian Gagnon

Abstract: The acidification of forest soils and surface waters and their relatively poor recovery record following reductions in atmospheric sulphur emissions is a major ongoing environmental problem, particularly in northeastern North America. The slow recovery of surface water is widely hypothesized to result from depletion of reservoirs of base cations in soil. This is concordant with the theory that the acid-neutralizing capacity (ANC) of lakes is likely proportional to the size of the exchangeable base cation reservoirs present in surrounding watershed soils. However, data describing these linkages are still nonexistent in the literature. Here we show that lake ANC is highly predictable ($r^2 = 0.75$) based on the size of the exchangeable Ca^{2+} reservoir in soil in 21 catchments representative of soil and lake conditions encountered in northeastern North America. This finding indirectly supports the hypothesis that the poor recovery of surface water from acidification is governed by the size of base cation reservoirs present in catchment soils. The size of the base cation reservoir in soil is thus a strong indicator of the acid–base status of both soils and surface waters.

Résumé : L'acidification des sols forestiers et des eaux de surface ainsi que leur récupération relativement mitigée malgré une diminution des dépôts atmosphériques de soufre représentent toujours un important problème environnemental, particulièrement dans le nord-est de l'Amérique du Nord. La faible récupération des eaux de surface a été principalement attribuée à la diminution des réservoirs de cations basiques dans les sols. Cela suppose que la capacité des eaux de surface à neutraliser les apports acides (CNA) est proportionnelle à la taille des réservoirs de cations basiques échangeables dans les sols des bassins versants. Bien que cette hypothèse paraisse plausible, elle n'a pas encore été démontrée. Dans cette étude, nous démontrons que la CNA des lacs peut être prédite avec succès ($r^2 = 0,75$) à partir de la taille du réservoir échangeable de Ca^{2+} pour 21 bassins versants forestiers représentatifs des conditions lacustres et édaphiques rencontrées dans le nord-est de l'Amérique du Nord. Cette découverte supporte indirectement l'hypothèse selon laquelle la faible amélioration de la CNA des eaux de surface est contrôlée par la taille des réservoirs échangeables de cations basiques présents dans le sols. Ces derniers sont donc des indicateurs fiables du statut acido–basique non seulement des sols mais aussi des eaux de surface.

Introduction

Since the 1980s and 1990s, there has been a 35%–45% reduction in atmospheric SO_2 emissions in the US and Canada as a result of bilateral regulations to control air pollution (Butler et al. 2000). This has led to a decrease in sulphur depositions and rain acidity and has fostered an interest in the possibility of reversing acidification in forest soils and surface waters. However, the capacity of forest soils to recover may be impaired by the large base cation losses they experienced in recent decades (Kirchner and Lydersen 1995; Houle et al. 1997; Lawrence et al. 1997). For instance, at the Hubbard Brook Experimental Forest in New Hampshire, as a legacy of decades of acidic deposition, the Ca^{2+} exchangeable reservoir in soil was severely depleted, lessening the potential for soil and surface water recovery and threatening the long-term sustainability of this ecosystem (Likens et al. 1996). Although some water bodies are responding to reductions in acidifying emissions and showing improvements in their acid-neutralizing capacities (ANCs), particularly in Europe, a large number are still not recovering or are recovering at a slower rate than expected in northeastern North America (Likens et al. 1996; Stoddard et al. 1999; Driscoll et al. 2001). The predominant hypothesis found in the litera-

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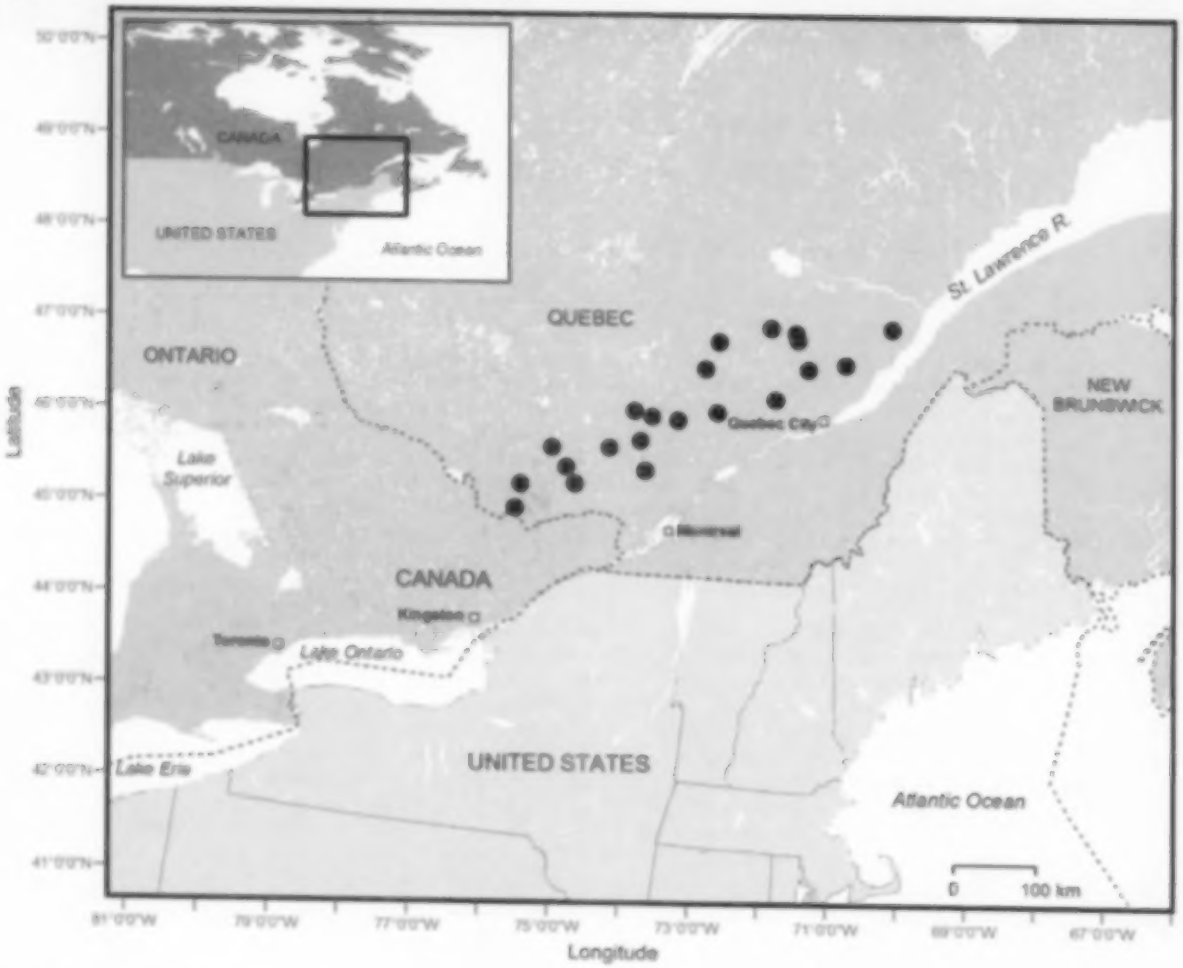
Fig. 1. Location of the 21 catchments in the province of Quebec, Canada.



ture is that the poor recovery of surface water chemistry is related to a drop in acid-neutralizing base cation reservoirs present in catchment soils (Likens et al. 1996; Stoddard et al. 1999; Driscoll et al. 2001), which would determine the extent to which surface waters are able to resist (or recover from) acid deposition. This implies that the ANC of surface water is governed by the size of the exchangeable base cation reservoir in the surrounding soils. Such a relationship might appear likely, but its existence has never been verified. Cycling of base cations, particularly Ca^{2+}, has been extensively studied in some calibrated catchments of northeastern North America (Johnson and Lindberg 1992; Likens et al. 1996; Houle et al. 1997). On the other hand, the results of temporal trends in surface chemistry exist for relatively extensive lake networks (Stoddard et al. 1999), but the necessary information on both soil and lake chemistry are often not available within an integrated research network for the same catchments. This has limited our ability to verify the above-mentioned hypothesis. Our objective is to test this hypothesis by examining the relationships between soil and headwater lake chemistry in 21 undisturbed forest catchments located in the south of the province of Quebec, Canada.

Materials and methods

The 21 headwater lakes are located within undisturbed forest catchments distributed within a ~90 000 km^2 area in the south of the province of Quebec, Canada (Fig. 1). In the summer and fall of 2001 and 2002, three soil pits were dug to a depth of 1 m within each catchment. The soil pits were dug ~50 m from the lakeshore and were evenly distributed around the lake perimeter. Every soil horizon thicker than 4 cm was sampled individually. Core samples were taken from each main soil horizon (diameter, 53 mm; length, 60 mm) to determine bulk density. Samples were air-dried and sieved to 2 mm. Exchangeable cations (Ca^{2+}, Mg^{2+}, K^+) were extracted with an unbuffered NH_4Cl (1 mol·L^{-1}, 12 h) solution and measured using inductively coupled plasma emission. Horizon thickness, bulk density, and coarse fragment content were used to convert the concentration of exchangeable cations in the distinct soil layers to kilograms

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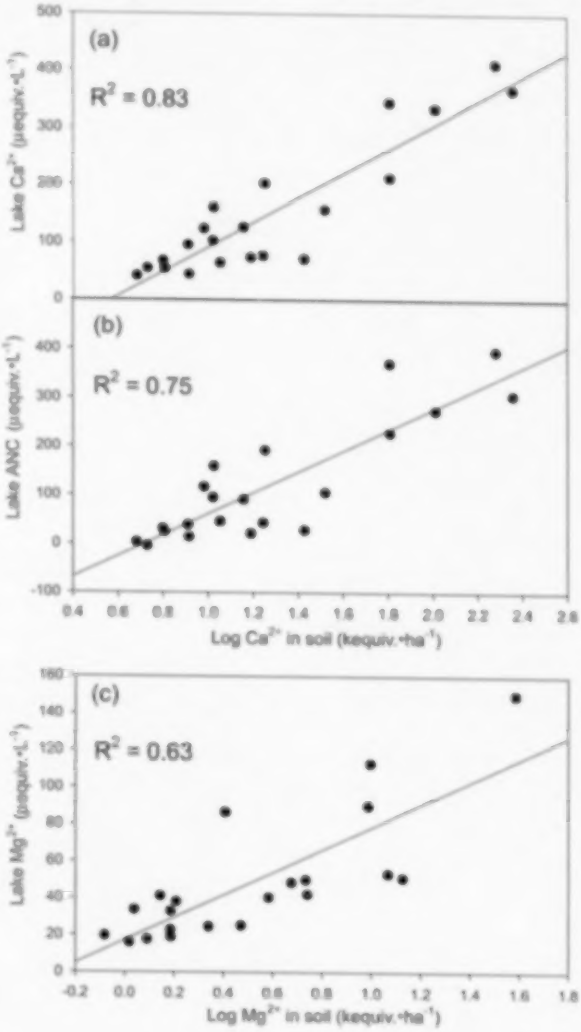
per hectare down to the C horizon (see Houle et al. (1997) for more details on soil sampling and chemical analysis). The size of the exchangeable cation (Ca^{2+}, Mg^{2+}, K^+) reservoir within the mineral soil (up to the C horizon) was chosen as a key predictive variable because it combines variations in exchangeable cation concentrations of distinct soil horizons, as well as variations in soil thickness, bulk density, and stone content. The average standard error (as percentage of the mean) of the exchangeable soil reservoir sizes was 17%, 28%, and 30% for K^+, Mg^{2+}, and Ca^{2+}, respectively. The lakes are part of a monitoring network and have been sampled regularly since 1984. The average lake and catchment size were 17 ha and 104 ha, respectively. For the purpose of this exercise, lake chemistry data for 2001–2003 (n = 6) were considered to coincide with the time of soil sampling, except for two lakes for which the 1984–1992 data were used because recent data were not available (see Houle et al. (2004) for more details on lake sampling and chemical analysis). Base cation lake concentrations and ANC exhibit low variability, with standard errors of 4.5%, 3.5%, 3.4%, and 4.0% for K^+, Mg^{2+}, Ca^{2+}, and ANC, respectively.

Results and discussion

The range of variations in soil of exchangeable Ca^{2+} (4.8–227.4 kequiv.·ha^{-1}), Mg^{2+} (0.83–38.6 kequiv.·ha^{-1}), and K^+ (0.4–4.4 kequiv.·ha^{-1}) reservoirs, as well as lake concentrations of Ca^{2+} (41.4–412.2 μequiv.·L^{-1}), Mg^{2+} (15.6–149.8 μequiv.·L^{-1}), K^+ (2.0–13.6 μequiv.·L^{-1}), and ANC (–4.4–396.5 μequiv.·L^{-1}), covers the range encountered in most soils and surface waters of northeastern North America (Johnson and Lindberg 1992; Stoddard et al. 1999). Thus we consider our study sites to be representative of this larger region, which is known to be particularly sensitive to acid rain. Lake concentrations of Ca^{2+}, Mg^{2+}, and K^+ were regressed (stepwise forward) individually against the size of their respective exchangeable reservoirs in soil and physical catchment properties (lake and basin area, drainage ratio of terrestrial to lake areas, lake perimeter, catchment slope, and lake water residence time). Among all the variables tested, a simple explicative model including only the size of the exchangeable Ca^{2+} reservoir in soil was by far the strongest predictor of lake Ca^{2+} (r^2 = 0.83, p < 0.001; Fig. 2*a*). Lake Mg^{2+} was also significantly predicted by the size of the exchangeable Mg^{2+} reservoir in the soil, although a weaker relationship was found (r^2 = 0.63, p < 0.001; Fig. 2*c*). The relationship between soil K^+ and lake K^+ was different: in addition to being predicted by the size of the exchangeable K^+ reservoir in the soil, predicting the lake K^+ concentration was improved by including catchment elevation in the explicative variables (r^2 = 0.50, p < 0.01, lake K^+ = 8.04 + soil K^+ × 1.0 – 7.7 × elevation (km)). Although the link with catchment elevation is not clear, it probably reflects a gradient in vegetation (from deciduous to coniferous stands) and temperature, which superimposes on an elevation gradient from the southwest to the northeast of the study area.

The nonlinearity (log scale for soil reservoir sizes) of the relationship between Ca^{2+} (Fig. 2*a*) and Mg^{2+} (Fig. 2*c*) in the soil and their respective lake concentrations indicates that lake Ca^{2+} and Mg^{2+} concentrations tend to reach a plateau when the size of the soil reservoir for Ca^{2+} and Mg^{2+} increases above a given value. Soil chemistry likely governs lake chemistry via its control of soil solution chemistry. This nonlinear relationship can thus be explained by the cation exchange dynamics between soil-adsorbing surfaces and soil solution, which is controlled by cation selectivity, soil exchange equilibrium function, salt concentration, and pH (Bohn et al. 1985). Cation exchange equations (Kerr-type exchange equations, e.g., Gains-Thomas, Gapon) show that divalent cation concentrations in the soil solution are a nonlinear function of their exchangeable concentrations in soils, reaching an asymptote, whereas soil base saturation continues to

Fig. 2. Relationships between exchangeable Ca^{2+} (log scale) in soil and (*a*) lake Ca^{2+} and (*b*) lake acid-neutralizing capacity (ANC) and (*c*) between exchangeable Mg^{2+} (log scale) in soil and lake Mg^{2+}.



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increase. The fact that lake K^+ concentrations, as opposed to Ca^{2+} and Mg^{2+} concentrations, follow a linear relationship with the size of the K^+ reservoir in soil also agrees with the ion exchange theory, K^+ having a much lower affinity than Ca^{2+} and Mg^{2+} for soil exchange sites and being controlled mainly by biotic processes in forested catchments. It also explains the weaker prediction of lake K^+ ($r^2 = 0.50$) compared with Mg^{2+} ($r^2 = 0.63$) and Ca^{2+} ($r^2 = 0.83$).

In accordance with the overall trend for northeastern North America (Stoddard et al. 1999), we observed a significant decrease in Ca^{2+} and Mg^{2+} concentrations in most of our lake network (Houle et al. 2004). Decreasing lake Ca^{2+} and Mg^{2+} concentrations were attributed to a decline in SO_4^{2-}, their main accompanying anion, which was being leached from catchments. A reduced leaching rate of base cations will in turn affect the size of exchangeable base cation reservoirs in soil. In fact, it may reduce the rate at which the reservoirs are emptying or even potentially increase their size if the rate of base cation replenishment from atmospheric deposition and weathering becomes greater than the losses resulting from tree uptake and the reduced soil leaching. Recovery of the most acidic soils, for instance, will translate into a higher proportion of cation exchange sites occupied by Ca^{2+} and Mg^{2+}, rather than H^+ and Al^{3+}, while at the same time, Ca^{2+} and Mg^{2+} concentration in soil solution will decrease. This indeed would change the slope of the relationship between the adsorbed and soil solution phases of Ca^{2+} and Mg^{2+}. Because the potential soil solution changes are expected to be reflected in lake chemistry, it follows that the relationships between absorbed soil cation and lake cation are not static over time and are expected to change, albeit over relatively long periods (e.g., decades).

Because Ca^{2+}, Mg^{2+}, and K^+ are major contributors to lake ANC, it follows that ANC can be predicted based on the size of the base cation reservoirs in soil. Lake ANC was therefore regressed against soil base cations and morphometric variables in the catchment. It was found that lake ANC was best predicted solely by the Ca^{2+} exchangeable reservoir size ($r^2 = 0.75$, $p < 0.001$; Fig. 2*b*). Soil Ca^{2+} was an expected key variable, because Ca^{2+} is an important contributor to lake's ANC in most surface waters in northeastern North America. In our data set of 21 lakes, the average contribution of Ca^{2+} to the total positive base cation loads (Ca^{2+}, Mg^{2+}, K^+, and Na^+) found in solution was 63%. Because ANC is a key variable in assessing the sensitivity of surface water, the data show that the capacity of a given lake to resist acidification is dependent on the size of the exchangeable Ca^{2+} reservoir within the surrounding soils. This finding has important implications, because acidification of surface waters, as well as the absence of recovery from acidification, has been widely hypothesized as being related to the relative size of base cation reservoirs in catchment soils (Likens et al. 1996; Stoddard et al. 1999; Driscoll et al. 2001). The relationship described here strongly supports this hypothesis and demonstrates that base cation reservoir size, particularly Ca^{2+}, is a strong indicator of the acid–base status of both soils and surface waters. When these considerations are added to the mounting evidence that basic cation reservoir size is also a predictor of tree growth and health (Shortle et al. 1997; Duchesne et al. 2002), our data strongly support the argument that soil base cation reservoirs should be designated as key variables in the management of terrestrial and aquatic ecosystems in forested areas.

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RAPID COMMUNICATION / COMMUNICATION RAPIDE

A field test verifies that pheromones can be useful for sea lamprey (*Petromyzon marinus*) control in the Great Lakes

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Abstract: Pheromone-baited traps have proven highly effective for managing insect pests by selectively removing reproductively active adults prior to mating. Here, we report a field test of two pheromones produced by the sea lamprey, *Petromyzon marinus*, which may be useful for controlling pest populations in the Laurentian Great Lakes. In the Trout River, Michigan, we demonstrated that (*i*) 90% of actively migrating sea lampreys could be drawn into streams treated with a migratory pheromone and (*ii*) lampreys were three times more likely to enter a barrier-integrated trap in a treated stream when pheromone was discharged directly through that trap (vs. an adjacent, unbaited trap). In a second experiment, we baited three traps with spermiating males (that are known to release a sex pheromone) to investigate how the quantity and spatial distribution of multiple pheromone signals would affect our ability to trap ovulating females. We found that mature females showed a strong tendency to select traps with multiple males over a trap with a single male when the signals were encountered simultaneously, but not when encountered sequentially. Our results strongly suggest pheromones may prove highly effective as attractants in trap-based management tactics for sea lamprey in the Great Lakes.

Résumé : Les es munis de phéromones se sont avérés très efficaces dans la lutte biologique contre les insectes ravageurs en retirant de façon sélective les adultes reproducteurs actifs avant l'accouplement. Nous décrivons ici un essai en nature de deux phéromones produites par la grande lamproie marine, *Petromyzon marinus*, qui pourraient servir au contrôle des populations nuisibles dans les Grands Lacs laurentiens. Dans la rivière Trout, Michigan, nous avons démontré que (*i*) 90 % des grandes lamproies marines en migration active peuvent être attirées vers des cours d'eau traités avec une phéromone de migration et que (*ii*) les lamproies sont trois fois plus susceptibles de s'introduire dans un piège intégré à une barrière dans un coureau traité lorsque la phéromone est introduite directement à travers le piège (par comparaison à un piège adjacent sans appât). Dans une deuxième expérience, nous avons placé dans trois pièges des mâles en phase de production de sperme (qui sécrètent alors une phéromone sexuelle) afin de déterminer comment la quantité et la répartition spatiale des signaux multiples de phéromones affectent la capture de femelles en ovulation. Lorsque les signaux sont perçus simultanément, les femelles matures montrent une forte préférence pour les pièges contenant plusieurs mâles par comparaison à un piège avec un seul mâle; cela ne se produit pas lorsque les signaux sont perçus en séquence. Nos résultats indiquent clairement que les phéromones pourraient être très efficaces comme appâts dans les stratégies de gestion par le piégeage des grandes lamproies marines dans les Grands Lacs.

[Traduit par la Rédaction]

Introduction

The sea lamprey, *Petromyzon marinus*, is a voracious parasite of the large-bodied fishes that inhabit the Laurentian Great Lakes and threatens a fishery valued at $1.55 billion per year (Ferreri and Taylor 1999). Traditional sea lamprey control has relied heavily on the use of the lampricide 4-nitro-3-(trifluoromethyl)phenol (TFM) to exterminate larvae prior to metamorphosis into the parasitic life stage. Though effective, costs for lampricide application are large, and del-

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ctericus effects on non-target species (e.g., lake sturgeon (*Acipenser fulvescens*)) have motivated control agencies to pursue alternatives to poisoning (Christie and Goddard 2003). The recent discovery that pheromones regulate specific migratory and reproductive behaviors of the sea lamprey has prompted much interest in testing their potential as a nontoxic and cost-effective alternative to lampricides (Li et al. 2003; Sorensen and Vrieze 2003). Although pheromones have been employed for over 30 years to control insect pests, this represents the first attempt to use vertebrate pheromones as part of an integrated pest management strategy.

Sea lampreys employ two pheromones to facilitate completion of their life cycle. In the spring of their last year of life, adult sea lampreys undertake nocturnal migrations into streams to spawn, attracted by a potent pheromone released by stream-resident, conspecific larvae (Sorensen et al. 2003, 2005). Presumably, this cue is an indicator of suitable rearing habitat that facilitates the process of stream-finding but does not result in natal homing (Sorensen and Vrieze 2003 and references therein). Migrating males typically arrive on the spawning grounds before females and establish nests. During the final stages of maturation (spermiation), male lampreys begin to release a sex pheromone that is highly attractive to ovulating females, signaling both reproductive readiness and nest location to potential mates (Li et al. 2002). Recent investigations aimed at understanding the behavioral responses of lampreys to these pheromones suggest three features of the system that make it useful for control: (*i*) small quantities of either pheromone elicit powerful behavioral responses; (*ii*) the pheromone cues remain active over large distances; and (*iii*) the compounds (or their analogs) may be synthesized at reasonable cost (Li et al. 2003; Sorensen and Vrieze 2003).

Twohey et al. (2003) hypothesized that as with insects, sea lamprey pheromones may be most effective as attractants to enhance the efficacy of traps. Here, we report the findings of two field experiments. The first was to determine (*i*) whether small additions of migratory pheromone would attract migrating adults to barriers in a natural stream and (*ii*) whether directing pheromone through a barrier-integrated trap would result in more captures vs. an adjacent, unbaited trap. In a second experiment, we sought to determine whether baiting freestanding traps in spawning grounds with spermiating males would effectively capture ovulating females. Johnson et al. (2005) recently demonstrated that ovulating females were attracted to male-baited traps in the absence of competing signals. We baited three traps with one, five, or ten spermiating males in two configurations to investigate how the quantity and spatial distribution of multiple sex pheromone signals would affect our ability to trap ovulating females. Together, these experiments constitute the first field test of management tactics that employ vertebrate pheromones.

Materials and methods

Migratory pheromone experiment

The sea lamprey migratory pheromone has three known components: petromyzonamine disulfate (PADS), petromyzosterol disulfate, and petromyzonal sulfate, which can be extracted from larval holding waters (Sorensen et al. 2005). We collected the whole pheromone from ~10 000 captive larvae using absorbent resins and established laboratory protocols (Sorensen et al. 2005; J.M. Fine, Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA, personal communication). Briefly, over a 5-month period we twice weekly turned off the water flowing into larval holding tanks for 24 h to accumulate odorants. To extract the pheromone, we pumped the holding tank water through 1 m long columns containing acrylic ester resin (XAD) at a rate of 0.5–1 L·min^{-1}, eluted the columns with methanol, and concentrated the solution by roto-evaporation at 35 °C. The final extract was stored at –80 °C until use. We measured only the concentration of PADS using mass spectrometry (the dominant and most active component; Sorensen et al. 2005), but have since verified that the other components were present in the expected proportions (J.M. Fine, personal communication).

On eight nights during the period 20 May – 11 June 2004, we quantified the differential attraction of sexually immature, migratory-phase sea lamprey into two similarly sized branches of the Trout River, a small tributary to Lake Huron in Michigan. The study area was located upstream of a low-head dam, and pre-experiment electrofishing surveys confirmed the absence of larval lampreys in or above the two branches. We enclosed a 200 m reach of the Trout River (150 m below the confluence with Klee Creek and 50 m above) with block nets and installed mesh barriers at the upstream ends. Each of the upstream barriers was fitted with two standard lamprey assessment traps. Twelve hours before the start of a trial, a new group of 20 lampreys (10 males + 10 females) fitted with passive integrated transponders (PIT tags) were placed into a holding cage at the bottom of the study area. We placed paired PIT detectors 50 m upstream of the holding cage (to determine how many lampreys moved upstream) and 15 m upstream of the confluence in each branch (to ascertain stream selection by each lamprey). One hour before sunset, the pheromone extract was pumped into one branch at the rate necessary to achieve a fully mixed concentration of 5×10^{-13} mol·L^{-1} of PADS. The branch receiving the pheromone was alternated on consecutive trials. To determine whether the pheromone could be used to effectively guide the lampreys into a trap, we added the pheromone directly into one of the two barrier-integrated traps, alternating between left- and right-bank traps in the treated branch between trials. At sunset, the lampreys were released and their passage across PIT antennas was monitored for 6 hours. We analyzed branch choice by fitting a main effects analysis of variance (ANOVA; STATISTICA 7.0, StatSoft Inc., Tulsa, Oklahoma) with pheromone (presence or absence), which branch was treated (Trout or Klee), and date (four equal periods) as design variables, and first branch entered as the response variable. We also tested for sex-related differences in branch choice with a χ^2 test. Differences in trap captures within the treated branch (treated trap vs. control trap) was tested with a Student's t test ($N = 7$). The final trial was excluded from the t test because of low water that prevented lampreys from entering the treated trap.

Sex pheromone experiment

In a 150 m section of the Ocqueoc River (Presque Isle County, Michigan), we placed three traps baited with

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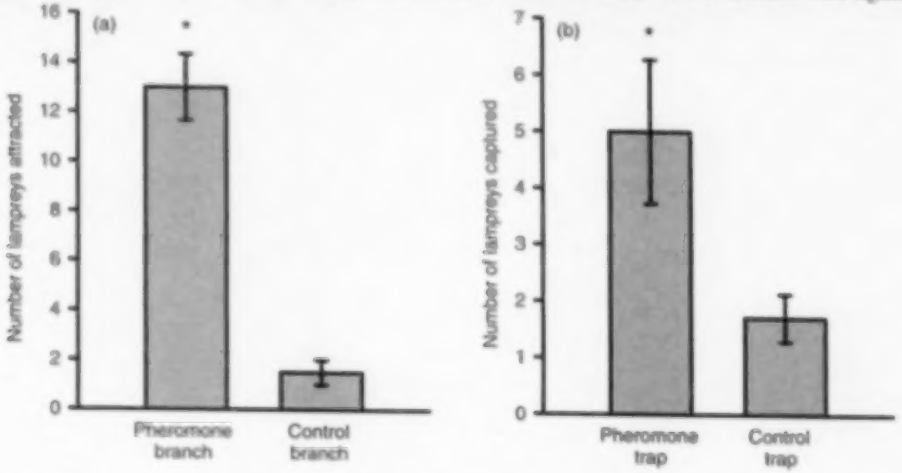
Fig. 1. Mean ± 1 standard error of the number of sea lampreys (*Petromyzon marinus*) (*a*) attracted into the branch of the Trout River treated with pheromone (main effects, analysis of variance, $P < 0.0001$) and (*b*) captured by the trap in that branch through which the pheromone was introduced (vs. an adjacent, unbaited trap) (main effects, t test, $P < 0.05$). Both differences were significant.



spermiating male lampreys (1 vs. 5 vs. 10) in either a cross-channel array ($N = 6$) or a longitudinal array ($N = 4$). Spermiating male lamprey are known to produce a pheromone, a principal component of which is 3-keto-petromyzonal sulfate (Li et al. 2002). To ensure the absence of competing pheromone signals, we located the study reach upstream of a permanent barrier in suitable spawning habitat. We fitted the three standard sea lamprey assessment traps with a small holding cage on the upstream end to house the spermiating males. During the cross-channel trials, we anchored the traps over a small cobble riffle, with approximately 2 m gaps between each trap and randomly assigned bait levels among the traps. During the longitudinal trials, we fixed the sequence with increasing bait moving upstream (one male, then five males, then ten males) to determine whether ovulating females would bypass a weak signal in preference for a stronger signal upstream. The traps were placed 10 m apart in the center of a straight portion of the stream with homogenous sandy substrate. Twelve hours before the start of each trial, we placed a new group of 10 ovulated female lampreys equipped with dorsal fin tags into a holding cage at the downstream end of the study area to acclimate to stream conditions. Following the acclimation period, the lampreys were released and left at large for 12 h. At the end of each trial, we emptied the traps and recorded the number and identity of each captured female. We analyzed for a main effect of bait level on trap capture success with one-way ANOVAs (STATISTICA 7.0, StatSoft Inc.).

Results and discussion

Migratory pheromone

Low concentrations of migratory pheromone in one branch of the Trout River were sufficient to attract 90% of actively migrating lampreys (Fig. 1*a*). On average, the pheromone-treated stream attracted 13.0 ± 1.3 lampreys (mean ± 1 standard error, SE), whereas the control stream only attracted 1.5 ± 0.5 lampreys. The remaining lampreys either did not move upstream (2.1 ± 1.0 lampreys) or stopped below the confluence of the two branches (3.4 ± 0.8 lampreys). There were no sex-related differences in the number of animals choosing either the treatment or control stream ($\chi^2 = 1.34$, degrees of freedom (df) = 1, $N = 116$, $P = 0.25$), and migratory pheromone presence was the only significant explanatory variable in the main effects ANOVA ($F = 65.5$, df = 1,10, $P < 0.0001$). Which branch was treated ($F = 0.07$, df = 1,10, $P = 0.80$) and date ($F = 1.42$, df = 3,10, $P = 0.29$) were nonsignificant factors. Slightly more than half of the migrating lampreys that chose the pheromone-treated branch were captured by one of the two traps (Fig. 1*b*). The pheromone-baited trap was responsible for 74% of the captures, averaging 5.0 ± 1.3 lampreys per trial (mean ± 1 SE) vs. 1.7 ± 0.4 lampreys in the adjacent, unbaited trap (t test: $t = 2.18$, df = 6, $P = 0.03$).

During the study period, discharges ranged from 0.11 to 0.32 $m^3 \cdot s^{-1}$ in the treated branch. Using an estimate of 30 $ng \cdot h^{-1}$ of PADS production by larvae housed in the laboratory (J.M. Fine and P.W. Sorensen, unpublished data), our treatment would have approximated the pheromone production from a larval population numbering between 5000 and 14 000 individuals. This concentration was sufficient to both strongly motivate stream selection and to lure individuals into a trap. Although we did not directly observe the behaviors of individual lamprey during the night trials, concentration gradients may have played a role in regulating lamprey movements. The two strongest pheromone gradients would have occurred cross-channel, first at the confluence of the two branches and then at the barrier in the treated branch. Some insects are known to track pheromone plumes by "casting" back and forth to sample across pheromone filaments, and gradients in pheromone strength often elicit stronger behavioral responses than more homogenous signals (Sorensen 1996). Sea lampreys have been observed vertically casting to locate river plumes (Sorensen and Vrieze 2003), and this tactic may be important at multiple decision points during the migration.

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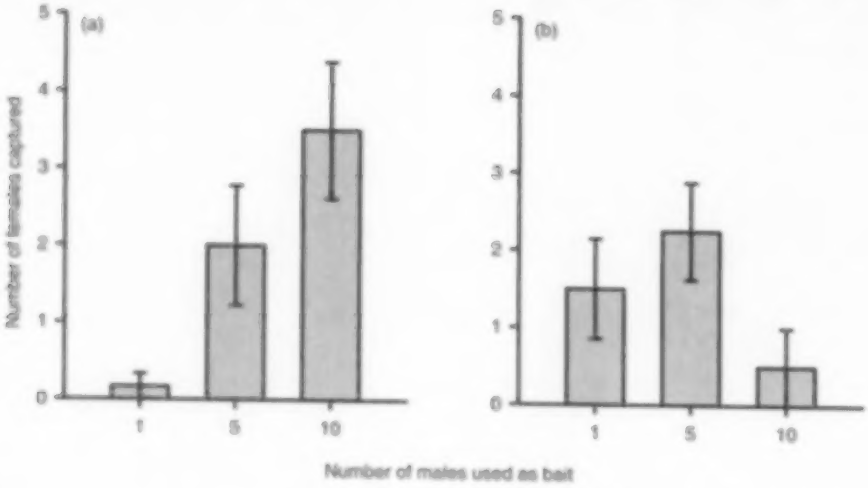
Fig. 2. Mean ± 1 standard error of the number of ovulating females captured by traps baited with spermiating males in (*a*) cross-channel (significant bait effect, analysis of variance (ANOVA), $P < 0.05$) and (*b*) longitudinal (no bait effect, ANOVA, $P = 0.17$) arrangements.



Sex pheromone

Increasing the number of spermiating males used as bait in freestanding traps resulted in more captures when the traps were arrayed across the channel (ANOVA: $F = 5.93$, $P = 0.01$; Fig. 2*a*), but not when arrayed longitudinally (ANOVA: $F = 2.18$, $P = 0.17$; Fig. 2*b*). The overall capture rate was somewhat higher in the cross-channel trials (mean ± SE, 5.7 ± 0.7 captures) than the longitudinal trials (4.3 ± 0.3 captures). These values represent a 43%–57% trapping efficiency (vs. unbaited traps that do not capture ovulating females; Johnson et al. 2005). Interestingly, the trap baited with a single male increased its capture rate from 3% of the total captures in the cross-channel array to 35% in the longitudinal array. In addition, the first two traps in the longitudinal array accounted for 88% of all captures, whereas the two similarly baited traps only accounted for 38% of the captures when placed cross-channel. In concert, these facts suggest the attractiveness of individual pheromone plumes was additive. Gradient strength may have also played a role in retaining lampreys in the vicinity of the first two traps in the longitudinal array. A searching female would have encountered a large change in signal strength when passing the second trap (*i.e.*, moving from a 15-male plume to a 10-male plume) vs. a small reduction of only one male when passing the first trap.

Implications for sea lamprey management

In the Great Lakes, sea lamprey populations are currently suppressed in many spawning streams through the application of lampricides. However, there are over 450 such streams in the basin, and many have populations that are too small or too dispersed to treat cost-effectively, but remain large enough to substantially contribute to the parasite population (Jones et al. 2003). In addition, there is a strong desire to develop new alternative control techniques that will allow an overall reduction in lampricide use. Our results clearly demonstrate that pheromones can be effectively used to attract and capture sea lampreys at multiple points during the spawning migration and will enhance integrated pest management of sea lamprey in the Great Lakes. For example, in streams where trapping has proven effective, catch rates are often low or variable in years following removal of the larval population (Moore and Schleen 1980). The addition of migratory pheromone to an existing barrier-integrated trapping system may increase capture efficiency and stabilize interannual variation in capture rates by ensuring a consistent signal strength is maintained in post-treatment years. Although this may ultimately recruit a larger spawning population below the barrier, sex pheromone-baited traps should prove effective at removing ripe females immediately prior to spawning. Similar attract and annihilate strategies have proven quite effective in managing many insect pests.

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Effects of reservoir connectivity on stream fish assemblages in the Great Plains

Jeffrey A. Falke and Keith B. Gido

Abstract: The upstream effects of reservoirs on stream fish assemblages were highly localized in 3rd- through 5th-order streams in the Great Plains, USA. Streams that differed in connectivity to reservoirs were sampled at their confluences with a river or reservoir and between the confluence and the stream's origin. Sites at confluences had higher total, nonnative, and reservoir species richness than middle sites. Variability in fish assemblage structure upstream of reservoirs was influenced by catchment area, stream size, gradient, and reservoir connectivity. Confluence sites connected to reservoirs were correctly classified based on the presence of red shiners (*Cyprinella lutrensis*) and bluntnose minnows (*Pimephales notatus*) and the absence of sand shiners (*Notropis stramineus*); middle sites on connected streams were classified by the absence of redfin shiners (*Lythrurus umbratilis*). Intensive sampling across pool habitats within two streams isolated by a reservoir indicated that abundance of common reservoir species was related to pool size, turbidity, and canopy cover, but not proximity to the reservoir. These data suggest that streams connected to reservoirs can maintain diverse native fish communities with minimal invasions by reservoir-dwelling species, but a fraction of the community either has been lost or occurs at low abundance (e.g., sand shiners and redfin shiners).

Résumé : Les effets de la présence de réservoirs sur les peuplements de poissons d'eau courante de l'amont sont très ponctuels dans des cours d'eau de 3^{e} à 5^{e} ordre dans les Grandes Plaines des É.-U. Nous avons échantillonné des cours d'eau ayant des connectivités diverses avec des réservoirs à leur point de confluence avec une rivière ou un réservoir et entre la confluence et l'origine du cours d'eau. Les sites de confluence ont une richesse en espèces plus élevée que les sites intermédiaires, en ce qui concerne les nombres totaux d'espèces, d'espèces non indigènes et d'espèces de réservoir. La variabilité dans la structure des peuplements de poissons en amont des réservoirs est influencée par la surface du bassin versant, la taille du cours d'eau, la pente et la connectivité au réservoir. Les sites de confluences rattachés aux réservoirs sont classifiés correctement par la présence de l'ide américain à nageoires rouges (*Cyprinella lutrensis*) et du ventre-pourri (*Pimephales notatus*) et par l'absence du méné paille (*Notropis stramineus*); les sites intermédiaires des cours d'eau rattachés aux réservoirs sont classifiés correctement par l'absence du méné d'ombre (*Lithrurus umbratilis*). Un échantillonnage soutenu dans les habitats de fosses dans deux cours d'eau isolés par un réservoir indique que l'abondance des espèces communes du réservoir est fonction de la taille des fosses, de la turbidité et de la couverture de la canopée, mais non de la proximité du réservoir. Ces données laissent croire que les cours d'eau rattachés aux réservoirs peuvent contenir des peuplements diversifiés de poissons indigènes avec des invasions minimales de poissons provenant des réservoirs; néanmoins, une fraction du peuplement peut être perdue ou se maintenir à de faibles densités; c'est le cas, par exemple du méné paille et de l'ide américain à nageoires rouges.

[Traduit par la Rédaction]

Introduction

Fragmentation of habitats by humans has negatively affected native biota worldwide (Noss and Csuti 1997), including species extinctions and alterations of community structure (Wilcox and Murphy 1985; Saunders et al. 1991). Stream organisms, which are heavily reliant on transport processes (e.g., Vannote et al. 1980), are particularly affected by breaches in connectivity that alter ecosystem processes (Ward 1983) and lead to isolation. In North America, nearly every major river basin contains an impoundment (Benke 1990). However, most impoundments in North America are relatively young (<30 years old), and there is little information on the long-term consequences of dams on stream fish communities.

Dams negatively affect native fishes in downstream reaches by altering habitat (Berkman and Rabeni 1987), thermal regimes (Vanicek et al. 1970; Holden and Stalnaker 1975), and flow regimes (Cushman 1985; Bain et al. 1988) and by facilitating introduced species (Marchetti and Moyle 2001; Propst and Gido 2004). Whereas upstream effects of dams are poorly understood (Pringle 1997), recent studies have reported changes in fish assemblage structure associated with stream bank destabilization (Penczak 2004), increased rich-

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ness of fish macrohabitat generalists (Herbert and Gelwick 2003), decreased juvenile fish survival (Ponton and Copp 1997), and decreased native fish diversity (Reyes-Gavilan et al. 1996) in streams above reservoirs.

In the Great Plains, reservoir density is high, and the potential for negative impacts by dams on native fish assemblages through disruption of connectivity is widespread. Many prairie stream fishes are negatively affected by the upstream effects of dams because of their life history attributes (Luttrell et al. 1999; Lienesch et al. 2000). For example, species with drifting larvae rely on large reaches of free-flowing river habitat and are negatively affected when their larvae or eggs drift into a reservoir and are either consumed by predators or settle to the substrate (Winston et al. 1991). In addition, bait-bucket or sportfish introductions in reservoirs can spread to connected streams (Gido et al. 2004). Thus, identifying changes in abundance and distribution of native and introduced species in relation to reservoir connectivity is critical for conservation of native fishes in the Great Plains.

We investigated fish assemblage structure in streams that differed in their connectivity with reservoirs. Our objectives were (*i*) to investigate if fish assemblage structure differed among streams with different connectivity levels to reservoirs and (*ii*) to quantify factors that influence fish assemblage structure within two tributary streams that were directly connected to a reservoir. We predicted that nonnative and common reservoir species richness would be highest in streams that were directly connected to reservoirs because of migration from the reservoirs and that native species richness would be lowest in these streams because isolation would lead to increased extinction rates. Thus, our second objective is based on the premise that in streams directly flowing into a reservoir, fish assemblages would be highly structured along a gradient of spatial proximity to the reservoir. In addition, nonnative and common reservoir species abundance was predicted to decline in isolated streams as distance from a reservoir increased.

Methods

Study area

Study streams were located within the Flint Hills ecoregion (Omernik 1987) located in northeastern Kansas, USA (Fig. 1). Geology in the region consists mainly of shale and cherty limestone, resulting in shallow, rocky soils. Because of this geology, agriculture (row crop farming and small grain farming) within the region is restricted to floodplain areas, and the remaining land cover within the study catchments was dominated by grasses ($\bar{x}$ = 66.5%; Table 1). Mean proportion of small grain and row crop agriculture was 24.2%, and the combined land under urban, forest, and other uses was <7% for all catchments. When compared with catchments dominated by agriculture, stream water quality in the Flint Hills is relatively pristine (Dodds and Oakes 2004).

Our reservoir impacted streams drained into either Milford Reservoir (6257 ha) or Tuttle Creek Reservoir (6676 ha; Fig. 1). Milford Reservoir impounds the Republican River and was constructed in 1967. Tuttle Creek Reservoir impounds the Big Blue River and was completed in 1959. These reservoirs are both operated by the US Army Corps of Engineers and their primary uses are water storage, flood control, and recreation.

Effects of reservoir connectivity among streams

To test the effects of reservoirs on fish assemblage structure, study streams were selected based on two factors: connectivity with a reservoir and distance from a confluence (Fig. 1). This resulted in a 3 × 2 classification scheme (two levels of distance from a confluence nested within three levels of connectivity). Directly connected streams had their confluence within the body of a reservoir (i.e., in a cove). Indirectly connected streams had their confluence with the flowing main stem of the impounded river, upstream of a reservoir. Control streams were not connected to a reservoir and had their confluence with the unimpounded Kansas River. Forty-one sites on 20 streams were selected, and geographic information system (GIS) coverage was used to quantify physical attributes of those sites. Streams selected were wadeable (maximum depth typically <1.5 m) and had similar stream size, catchment land use, and catchment surficial geology. Stream order was calculated from a modified version of the National Hydrography Dataset (US Geological Survey 1997), and surficial geology was based on soil measurements obtained from the STATSGO database (Natural Resources Conservation Service 1994). Land cover was characterized for each catchment using the National Land Cover Database (US Geological Survey 1994) by calculating proportions of each land-use category within a catchment (Table 1). Sites on study streams also were selected based on longitudinal position. Middle sites were approximately midway (4.4–15.8 km, $\bar{x}$ = 11.0, standard error (SE) = 1.3) between the stream's origin and its confluence with a river or reservoir. Confluence sites were at the confluence of the stream with a reservoir or river. Downstream ends of directly connected confluence sites were located approximately where streamflow subsided. For indirectly connected and control streams, the downstream end of confluence sites was located at the confluence of the stream and river.

Fish assemblage data for 17 of the 41 sites were collected by the Kansas Department of Wildlife and Parks (KDWP) during summers from 1995 to 2003. Of those 17, four were indirectly connected to a reservoir (three middle, one confluence), five were directly connected (three middle, two confluence), and eight were control sites (five middle, three confluence). The other 24 sites were visited between July and September 2003 and were paired middle and confluence sites. At each site, a reach 40 times the mean stream width (minimum 150 m, maximum 300 m) was sampled. This allowed for equal effort per unit of area (Lazorchak et al. 1998). Sites were blocked with nets (4.7 mm mesh) at the upstream and downstream ends, and fishes were collected using a pulsed-DC backpack electrofishing unit and seines (4.7 mm mesh). One upstream electrofishing pass was made, and one downstream pass was made seining suitable habitats. Fishes >200 mm total length (TL) were identified in the field and released. Fishes ≤200 mm TL were preserved in 10% formalin, returned to the laboratory, and transferred to 70% isopropyl alcohol for sorting and identification.

Data analysis focused on both qualitative (presence or absence) and quantitative (abundance) changes in fish community structure, with a specific evaluation of changes in the

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Fig. 1. Locations of sample sites (*a*) within streams (N = 22 pools) and (*b*) among streams (N = 41 sites) in the Flint Hills, Kansas, USA. (*c*) The shaded region within Kansas represents the Flint Hills ecoregion (Omernik 1987). (*d*) The position of Kansas within the continental United States is shown. Among streams (*b*), solid symbols represent confluence sites; open symbols represent sites halfway up the perennially wetted length of the stream; squares are directly connected streams; diamonds are indirectly connected streams; and circles are control streams. Within streams (*a*), pool locations are represented by solid circles. Location of 2003 middle and confluence sites are provided for reference (solid squares, confluence sites; open squares, middle sites).

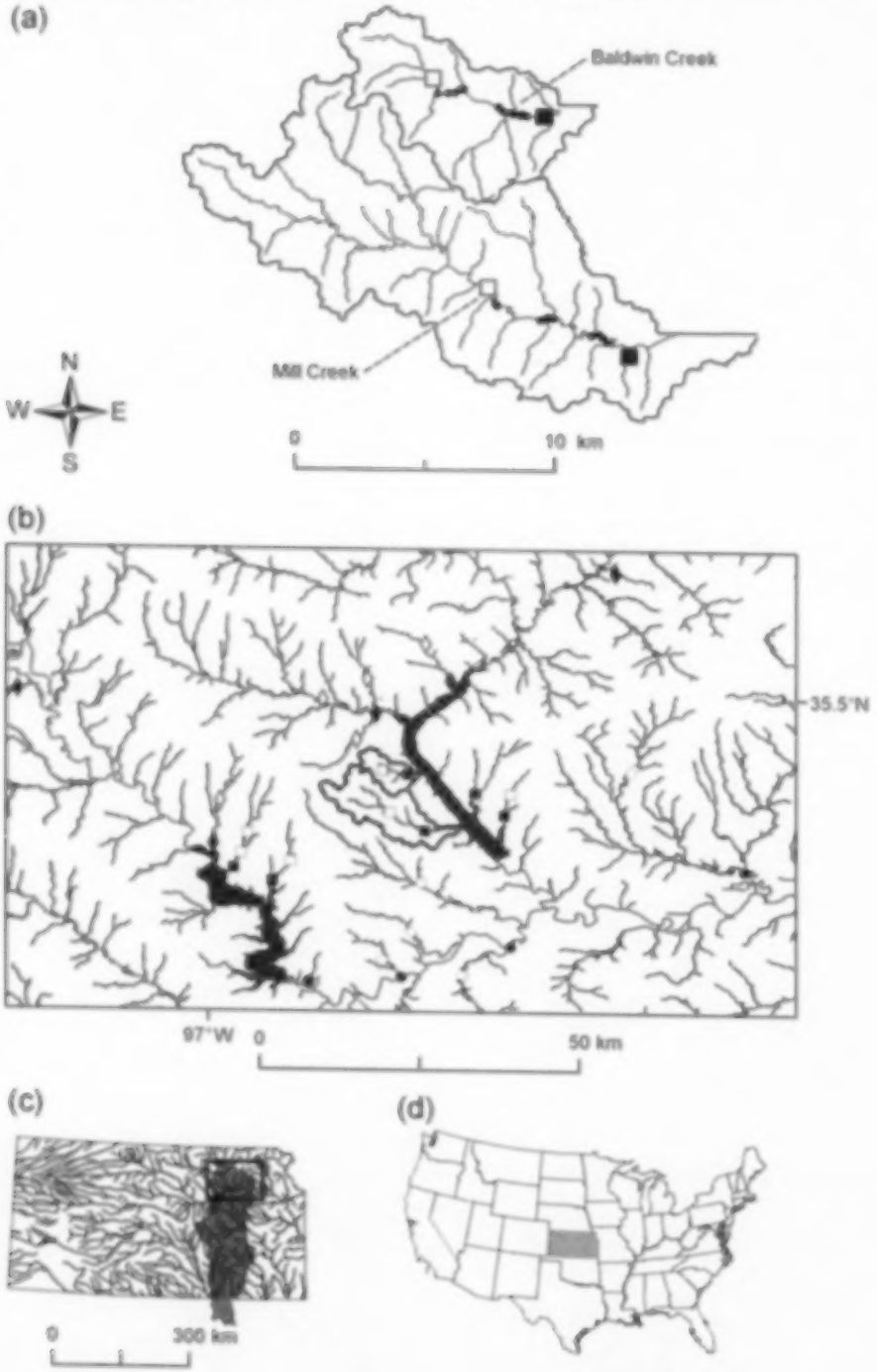

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Table 1. Study streams, connectivity category (DC, directly connected; IC, indirectly connected; CT, control), catchment area (km^2), Strahler order, and proportion of within-catchment land uses estimated using a geographic information system.

				Land uses					
Stream	Connectivity category	Catchment area (km^2)	Strahler order	Water	Urban	Forest	Grasslands	Agriculture	Wetlands
Baldwin	DC	34.00	3	2.11	0.61	7.64	72.21	14.84	0.83
Carnahan	DC	89.62	3	1.55	0.20	5.75	75.13	14.52	0.30
Cedar	IC	179.66	3	0.39	0.01	2.74	57.06	38.32	0.74
Fancy	IC	473.44	5	0.28	0.04	0.98	55.52	42.10	0.44
Fourmile	CT	23.67	3	1.19	3.39	6.12	64.93	20.91	0.48
Huntress	IC	79.19	4	0.17	0.93	0.81	46.90	49.90	0.25
Kitten	CT	14.65	3	0.40	0.82	7.34	76.60	13.94	0.42
Madison	DC	47.55	3	0.32	0.18	5.34	82.12	11.22	0.29
Mall	IC	116.96	3	0.65	0.18	1.59	57.01	39.49	0.48
McDowell	CT	268.26	4	0.42	0.36	2.14	77.74	11.61	0.35
McIntyre	DC	62.67	3	2.75	0.04	3.25	79.57	8.66	0.36
Mill	DC	106.72	3	1.60	0.20	5.25	63.95	26.46	0.48
Mulberry	IC	26.55	3	0.03	0.41	3.15	55.60	40.49	0.14
North Otter	IC	71.08	4	0.24	0.00	2.44	65.40	31.32	0.33
Rock	CT	612.62	5	0.58	0.27	3.79	68.91	22.25	0.48
Sevenmile	CT	98.46	3	2.17	1.74	13.22	64.99	12.89	0.66
Swede	IC	90.64	3	0.51	0.01	4.42	66.63	27.49	0.41
Threemile	CT	74.04	3	0.48	4.09	15.08	69.41	3.13	0.32
Timber	DC	96.16	3	0.77	0.31	5.01	67.90	23.08	0.61
Walnut	IC	75.02	3	1.27	0.20	3.19	62.96	31.21	0.70
Mean	—	132.05	—	0.89	0.70	4.96	66.53	24.19	0.45
SE	—	34.28	—	0.17	0.25	0.83	2.05	2.92	0.04

Note: Water includes streams and impoundments. Urban includes high- and low-intensity residential and commercial transportation. Forest includes deciduous, evergreen, and mixed forests. Grasslands includes grasslands and pasture. Agriculture includes row crops and small grains. Wetlands includes woody and emergent/herbaceous wetlands. Means and standard error of the means (SE) are provided for each category.

abundance of facultative reservoir and nonnative species. We identified facultative reservoir species in our collections as those that typically occur, or are stocked, in reservoirs and may only require streams for a portion of their life history. These species were identified by a combination of field collections (J. Falke, unpublished data) and a review of species accounts from reservoirs in this region (Eberle et al. 2000; Gido et al. 2002*a*; Table 2). Nonnatives were classified based on distribution information given in Cross (1967) and Cross and Collins (1995) (Table 2).

Multivariate analysis of variance (MANOVA) was used to test for effects of reservoir connectivity (directly connected, indirectly connected, and control) and longitudinal position (middle or confluence) on total species richness, native species richness, nonnative species richness, and reservoir species richness. If the overall MANOVA was significant ($\alpha = 0.05$), then relationships within the four richness categories were then tested using two-way analysis of variance (ANOVA). Because of multiple comparisons among the four richness categories, differences were considered significant at a Bonferroni-adjusted α level ($\alpha = 0.05/4 = 0.0125$).

Although we attempted to match streams based on habitat and land use of stream segments, we used redundancy analysis (RDA) to evaluate the relationship between catchment-scale environmental variables (see Table 3 for list of variables) and spatial variation in fish assemblage structure. RDA is a canonical form of principal components analysis (PCA) that selects a linear combination of environmental variables to maximize the dispersion of species scores (ter Braak 1995). This analysis produces a diagram with vector arrows that represent the relative importance of environmental factors in describing variation in the fish assemblage. Monte Carlo simulations (500 iterations) were used to test whether eigenvalues from the RDA were significantly ($P \leq 0.05$) greater than those generated from a randomized matrix. Our analysis was first conducted using the entire data set. We expected that differences would be apparent between confluence and middle sites because of longitudinal variation in stream size and associated physical and chemical properties within a given stream. Subsequently, we conducted RDA on confluence and middle sites separately to evaluate if reservoir connectivity explained a large proportion of the variation in assemblage structure. To isolate the amount of variation explained by connectivity to the reservoir, we used a partial RDA (ter Braak 1995) in which physical habitat variables served as covariates and the ordination was only constrained by connectivity. A Monte-Carlo procedure (500 iterations) was performed to test if the RDA axes were significantly different from random. We used RDA instead of other multivariate ordination techniques (e.g., canonical correspondence analysis) because of the short gradient lengths of our measured environmental variables (ter Braak and Šmilauer 2002).

Discriminant function analysis (DFA) was used to complement the RDA by specifically identifying species that could be used to classify streams into reservoir connectivity groups. This analysis can potentially detect more subtle differences in assemblage structure among stream types than

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Table 2. Relative abundance (proportion among total collected), number of sites occupied, and presence and absence for fish species collected at 41 sites classified by connectivity (CT, control; IC, indirectly connected; DC, directly connected) and longitudinal position (CFL, confluence, MID, middle) in the Flint Hills, Kansas, USA.

						CT		IC		DC	
Scientific name	Common name	Code	Category	Sites occupied	Relative abundance	CFL	MID	CFL	MID	CFL	MID
Ameiurus melas	Black bullhead	AMEMEL	N	20	0.52	×	×	×	×	×	×
Ameiurus natalis	Yellow bullhead	AMENAT	N	25	0.32	×	×	×	×	×	×
Aplodinotus grunniens	Freshwater drum	APLGRU	N, R	6	0.05			×		×	
Campostoma anomalum	Central stoneroller	CAMANO	N	37	21.99	×	×	×	×	×	×
Carpiodes carpio	River carpsucker	CARCAR	N, R	11	0.23	×	×	×	×	×	
Carpiodes cyprinus	Quillback	CARCYP	N, R	2	0.02	×					
Catostomus commersonii	White sucker	CATCOM	N	28	0.56	×	×	×	×	×	×
Cyprinella lutrensis	Red shiner	CYPLUT	N	37	22.51	×	×	×	×	×	×
Cyprinus carpio	Common carp	CYPCAR	R, I	17	0.36	×	×	×		×	×
Dorosoma cepedianum	Gizzard shad	DORCEP	N, R	12	2.89	×		×		×	
Etheostoma nigrum	Johnny darter	ETHNIG	N	18	0.57	×	×	×	×	×	×
Etheostoma spectabile	Orangethroat darter	ETHSPE	N	37	5.06	×	×	×	×	×	×
Gambusia affinis	Western mosquitofish	GAMAFF	I	18	3.86	×	×	×	×	×	×
Ictalurus punctatus	Channel catfish	ICTPUN	N, R	19	0.23	×	×	×	×	×	×
Ictiobus bubalus	Smallmouth buffalo	ICTBUB	N, R	9	0.20	×		×		×	
Ictiobus cyprinellus	Bigmouth buffalo	ICTCYP	N, R	11	0.80	×		×		×	
Lepisosteus osseus	Longnose gar	LEPOSS	N, R	11	0.12	×	×	×		×	×
Lepisosteus platostomus	Shortnose gar	LEPPLA	N	2	0.01	×				×	
Lepomis cyanellus	Green sunfish	LEPCYA	N	38	2.99	×	×	×	×	×	×
Lepomis humilis	Orangespotted sunfish	LEPHUM	N	25	2.80	×	×	×	×	×	×
Lepomis macrochirus	Bluegill	LEPMAC	R, I	27	1.73	×	×	×	×	×	×
Lepomis macrochirus × *Lepomis cyanellus*	Bluegill × green sunfish hybrid	LEPHYB	—	5	0.05	×		×			
Lepomis megalotis	Longear sunfish	LEPMEG	N	9	0.48	×	×	×			
Lepomis microlophus	Redear sunfish	LEPMIC	I	1	0.01	×				×	
Luxilus cornutus	Common shiner	LU×COR	N	21	5.01	×	×	×	×	×	×
Lythrurus umbratilis	Redfin shiner	LYTUMB	N	19	4.00	×	×	×	×		
Micropterus salmoides	Largemouth bass	MICSAL	R, I	26	1.09	×	×	×	×	×	×
Morone chrysops	White bass	MORCHR	N, R	9	0.57	×		×		×	
Moxostoma erythrurum	Golden redhorse	MOXERY	N	2	0.01	×	×				
Moxostoma macrolepidotum	Shorthead redhorse	MOXMAC	N	8	0.10	×	×	×		×	×
Notemigonus crysoleucas	Golden shiner	NOTCRY	R, I	5	0.03			×	×		×
Notropis atherinoides	Emerald shiner	NOTATH	R, I	6	0.05			×		×	
Notropis percobromus	Carmine shiner	NOTPER	N	20	1.06		×				
Notropis stramineus	Sand shiner	NOTSTR	N	3	1.08	×	×	×	×	×	×
Notropis topeka	Topeka shiner	NOTTOP	N	1	0.05	×			×		
Noturus exilis	Slender madtom	NOTEXI	N	10	0.17		×		×		×
Noturus flavus	Stonecat	NOTFLA	N	13	0.19	×	×	×	×		×
Percina caprodes	Logperch	PERCAP	N	15	0.14	×	×	×	×	×	×
Phenacobius mirabilis	Suckermouth minnow	PHEMIR	N	23	0.62	×	×	×	×	×	×
Phoxinus erythrogaster	Southern redbelly dace	PHOERY	N	7	5.26		×		×		

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Table 2 (*concluded*).

Scientific name	Common name	Code	Category	Sites occupied	Relative abundance	CT		IC		DC	
						CFL	MID	CFL	MID	CFL	MID
Pimephales notatus	Bluntnose minnow	PIMNOT	N	35	6.61	×	×	×	×	×	×
Pimephales promelas	Fathead minnow	PIMPRO	N	24	0.61	×	×	×	×	×	×
Pimephales vigilax	Bullhead minnow	PIMVIG	R, I	9	0.27	×	×	×		×	
Pomoxis annularis	White crappie	POMANN	R, I	10	1.02	×	×	×	×	×	×
Pomoxis nigromaculatus	Black crappie	POMNIG	N, R	1	<0.01					×	
Pylodictus olivaris	Flathead catfish	PYLOLI	N, R	3	0.01	×	×	×			
Sander vitreus × *Sander canadensis*	Saugeye	SANHYB	R, I	5	0.03			×	×	×	
Semotilus atromaculatus	Creek chub	SEMATR	N	29	3.64	×	×	×	×	×	×

Note: Codes are the first three letters of the genus and specific epithet. Analysis categories: N, native; R, reservoir; I, introduced.

Table 3. Codes and descriptions of landscape-scale environmental variables.

Variable code	Variable description
WSHED	Catchment area (km^2)
STRAHLER	Strahler stream order
GRADIENT	Stream reach gradient ($m \cdot km^{-1}$)
WATER	Proportion of streams and impoundments in catchment
URBAN	Proportion of urban area in catchment
FOREST	Proportion of forested area in catchment
GRASS	Proportion of grasslands in catchment
AG	Proportion of agriculture in catchment
WET	Proportion of wetlands in catchment

RDA. DFA uses linear combinations of predictor variables to maximize the separation between groups (i.e., reservoir connectivity). DFA is an appropriate method for ecological classification of samples based on a suite of predictor variables (Legendre and Legendre 1998). Independent variables (i.e., species) that were unrelated to connectivity type or that were redundant with other variables were removed from the analysis with a stepwise procedure. For these analyses, variables with partial correlation coefficients with probability of F values < 0.05 were entered and those with $F > 0.10$ were removed. Within-group covariance matrices were used, and prior probabilities were computed from group sizes. All models were generated using SPSS® (version 11.0, SPSS Inc. 2001). Individual connectivity models were evaluated using a leave-one-out procedure, in which one site was excluded, a model was constructed using $n - 1$ sites, and the excluded site was predicted using this model.

Effects of reservoir connectivity within streams

Because our results indicated a localized effect of reservoirs on stream fish assemblages (see Results), we intensively sampled two streams that were directly connected to Tuttle Creek Reservoir during the summer 2004. Both streams, Baldwin Creek and Mill Creek, drain directly into Tuttle Creek Reservoir from the west (Fig. 1). We sampled fish assemblages and physical habitat in pools located at and between the confluence and middle sites sampled the previous year. Twelve pools were sampled on Baldwin Creek and 10 pools on Mill Creek (Fig. 1). Pools were blocked off with nets to prevent escape of fishes from the pool. One pass was made through each pool electrofishing suitable habitats (woody debris, boulders, rock piles, etc.) using a pulsed-DC backpack electrofishing unit. Then, each pool was seined until no additional species were captured (3–10 passes). Fishes >200 mm TL were identified in the field and released, and fishes ≤200 mm TL were preserved in 10% formalin and returned to the laboratory for sorting and identification.

We also measured physical habitat for each pool. Before fish collection, conductivity ($\mu S \cdot L^{-1}$) and temperature (°C) were measured using a YSI meter (model 30; YSI Incorporated, Yellow Springs, Ohio), and three water samples (500–1000 mL) were filtered (1 µm pore size) on site for total dissolved solids, organic matter, and inorganic matter. Following fish collection, we noted the presence or absence of small and large woody debris and emergent, submergent,

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and floating aquatic macrophytes. Canopy cover was quantified using a densiometer at three positions in the pool: upstream, middle, and downstream. Pool length (m) was measured along the thalweg of the pool, from the upstream block net to the downstream block net. Based on pool length, the width of five equally spaced transects perpendicular to streamflow were measured. Along each transect, depth and dominant substrate were recorded at five equally spaced points. Substrate was classified according to a modified Wentworth scale (Cummins 1962) as fines (<2 mm), gravel (2–15 mm), pebble (16–63 mm), cobble (64–256 mm), boulder (256–1024 mm), and bedrock (>1024 mm).

Before evaluating changes in fish assemblage structure in pools with increasing distance from a reservoir, we first quantified differences in physical habitat and assemblage structure between Mill and Baldwin creeks. Between-stream variability in physical habitat was evaluated with a discriminant function analysis with physical habitat measurements as independent variables. As above, classification success was evaluated using the leave-one-out cross-validation technique. We also were interested in testing whether physical habitat of pools varied as distance from a reservoir increased. For each stream, we summarized the physical habitat of pools with PCA and then used correlation analysis to quantify the association between reservoir distance and PCA axes scores. For this PCA, we focused scaling on inter-variable correlations, and variable scores were divided by their standard deviation for standardization. To remove effects of unit sizes within the physical habitat variables, we centered and standardized the variables before analyses.

To test for changes in assemblage structure with increasing distance from a reservoir, we chose two measures of similarity to compare assemblages in each pool with the fish assemblage structure in the pool closest to the reservoir. Jaccard's index of similarity (Jaccard 1908) was used to test for similarity in species presence or absence, and percent similarity index (PSI; Renkonen 1938) was used to test similarities in species relative abundances. PSI and Jaccard's similarity values were obtained using NTSYSpc software (version 2.10; Rohlf 2000).

Variation explained by proximity to the reservoir was quantified by partial RDA (ter Braak 1995) in which physical habitat variables served as covariates and the ordination was only constrained by reservoir distance (see above for partial RDA explanation). Finally, we used multiple regression to investigate the influence of physical habitat features on the abundance of reservoir species. The pooled abundance of reservoir species captured by backpack electrofishing and seining was used as the dependent variable for this analysis. Physical habitat variables and reservoir distance served as independent variables. We used stepwise forward selection ($P \leq 0.05$) to include significant variables in the model. SPSS software (version 11.0; SPSS Inc. 2001) was used for the multiple regression analysis.

Results

Effects of reservoir connectivity among streams

A total of 37 104 individuals representing 49 species was collected at the 41 sites. Minnows numerically dominated the collections; red shiners (*Cyprinella lutrensis*) were most abundant (22.51% of total individuals collected), followed by central stoneroller (*Campostoma anomalum*; 21.99%), and bluntnose minnow (*Pimephales notatus*; 6.61%) (Table 2). Green sunfish (*Cyprinella lutrensis*) were collected at the largest number of sites (38 sites), followed by central stoneroller (37 sites), orangethroat darter (*Etheostoma spectabile*; 37 sites), red shiner (37 sites), and bluntnose minnow (35 sites).

To evaluate the importance of temporal variation in our analysis, we ran our analysis with only the 2003 data (24 sites) and with the entire data set (41 sites). Because they yielded similar results, we only present results from the entire data set.

Results of the MANOVA suggested that the four richness categories did not significantly differ among stream connectivity types ($P \geq 0.34$), but they were significantly different between confluence sites and middle sites ($P \leq 0.021$). Bonferroni-corrected two-way ANOVAs showed higher total, nonnative, and reservoir richness at confluence sites than at middle sites (corrected P values ≤ 0.001) but no difference in native richness between confluence sites and middle sites (corrected $P = 0.084$). On average, there were six more species (30%) at confluence sites than at middle sites (Fig. 2), and this difference was most pronounced in directly connected streams. This was primarily due to the occurrence of reservoir species at confluence sites, which had 78%, or seven more reservoir species, on average, than middle sites. Nonnative species richness was also approximately 50% higher (two species) at confluence sites than at middle sites. Although not significant, directly connected streams had the highest mean nonnative and reservoir species richness among the connectivity categories, and total richness differences between confluence and middle sites were most pronounced in these streams, as predicted because of their isolation by the reservoir.

Redundancy analysis characterized the association between fish assemblage structure and habitat across the 41 sample sites (Fig. 3). Cumulatively, axis I and II explained 68.2% of the constrained variability in the fish assemblage across sites. Stream size, watershed area, and gradient were important explanatory variables in the RDA. Species typical of small, headwater streams (i.e., creek chub (*Semotilus atromaculatus*), southern redbelly dace (*Phoxinus erythrogaster*), and white sucker (*Catostomus commersoni*)) had low axis I scores and were found in sites with high gradients and small watershed areas. Reservoir species (i.e., gizzard shad (*Dorosoma cepedianum*), white bass (*Morone chrysops*), and saugeye (*Sander vitreus* × *Sander canadense*)) had high axis I scores and were typical of low-gradient, confluence sites. These differences in fish assemblage structure also resulted in a clear separation between middle and confluence site scores.

Axis I and II of the RDA used to characterize fish assemblage and habitat associations among the 18 confluence sites explained 67.0% of the constrained variability in the fish assemblage across sites (Fig. 4). Stream gradient, stream size, watershed area, and the proportion of agricultural land use within the catchment were important explanatory variables. Species characteristic of directly connected confluence sites

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Fig. 2. Mean (±1 standard error of the mean) (*a*) total species richness, (*b*) native species richness, (*c*) nonnative species richness, and (*d*) reservoir species richness among streams that differ in connectivity to a reservoir (DC, directly connected; IC, indirectly connected; CT, connected to the unimpounded Kansas River) and between longitudinal positions. Open bars represent sites at confluences, and solid bars represent sites halfway up the perennially wetted stream length.

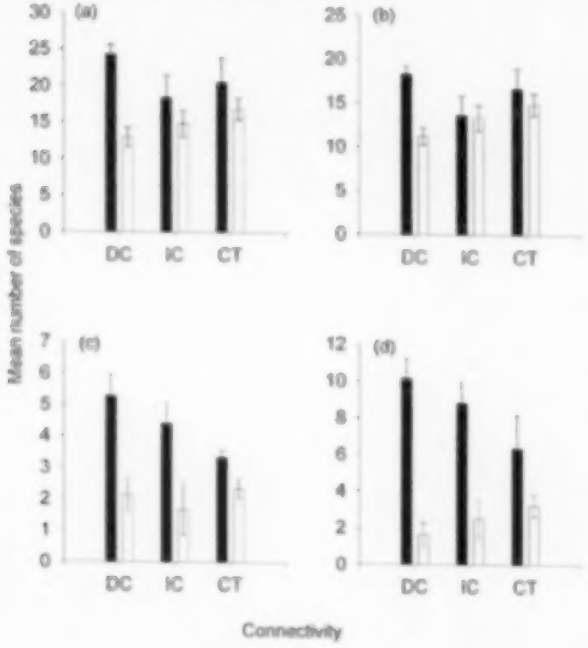
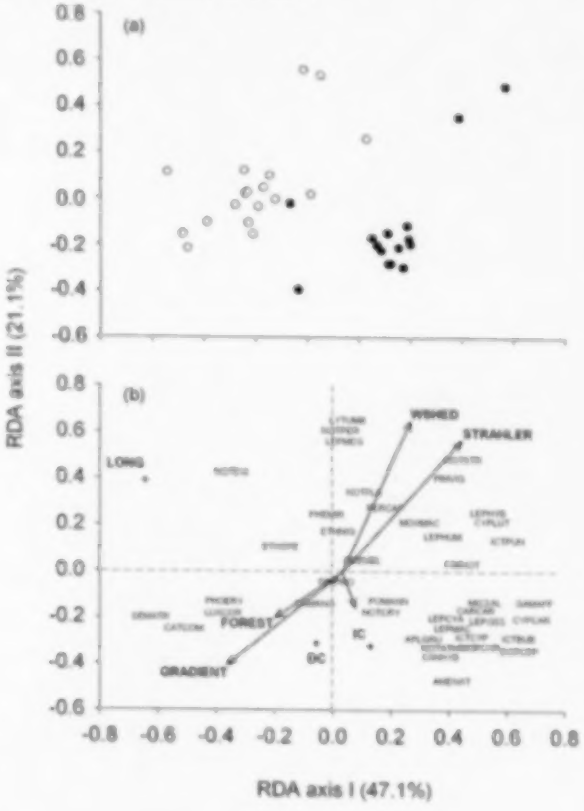


Fig. 3. Association of fish species and environmental variables, longitudinal position (LONG), and connectivity type (DC, directly connected; IC, indirectly connected) (*b*) from a redundancy analysis (RDA). Site scores are plotted in (*a*): ○, sites located halfway up the perennially wetted length of a stream; ●, confluence sites. Site and species vector arrows were deleted for clarity. Crosses (+) indicate binary variables used to detect treatment effects. Species codes are defined in Table 2; environmental variables are defined in Table 3.



included emerald shiner (*Notropis atherinoides*), river carpsucker (*Carpiodes carpio*), and golden shiner (*Notemigonus crysoleucas*) (all classified as reservoir species) and had low axis I species scores. Axis I also represented a gradient of stream size, with sites on smaller streams having high axis I site scores and sites on larger streams having low axis I scores (Fig. 4). In general, control sites had high axis II scores, whereas directly connected and indirectly connected sites had low to intermediate axis II scores. Axis II represented a gradient of watershed area (high axis II scores) and the proportion of agriculture within a watershed (low axis II scores). Connectivity in confluence sites was an important predictor of fish assemblage structure, as evidenced by a significant axis I ($F = 3.764$, $P = 0.001$) relationship between assemblage structure and connectivity when environmental variables were entered as covariables; however, the relationship with connectivity was not an important predictor in axis II ($F = 0.585$, $P = 0.384$).

Axes I and II of the RDA used to characterize fish assemblage and habitat associations among the 23 middle sites explained 64.2% of the constrained variability in the fish assemblage across sites (Fig. 5). Stream size, watershed area, and gradient were important explanatory variables. Species typical of headwater assemblages (i.e., central stoneroller, southern redbelly dace, orangethroat darter, and creek chub) had lower axis I scores, whereas relatively larger stream sites, characterized by species such as red shiner, redfin shiner (*Lythrurus umbratilis*), and sand shiner (*Notropis stramineus*), had higher axis I scores. Axis II represented a gradient between sites in watersheds with a high proportion of agriculture (low axis II scores) and sites with high gradients (high axis II scores). Site scores did not cluster according to reservoir connectivity in ordination space (Fig. 5), indicating weak effects of reservoir connectivity at middle sites. This was confirmed by nonsignificant relationships on RDA axes I and II between assemblage structure and connectivity when environmental variables were included as covariables ($P \geq 0.168$).

For confluence sites, 77.8% of sample sites were correctly classified according to reservoir connectivity using DFA. Directly connected and control sites were classified 100% correctly, but indirectly connected sites were only classified correctly for one of five sites (20%). Indirectly connected

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Fig. 4. Association of fish species environmental variables and connectivity type (DC, directly connected; IC, indirectly connected) (*b*) at confluence sites from a redundancy analysis (RDA). Site scores are plotted in (*a*): ◇, directly connected sites; ■, indirectly connected sites; ●, control sites. Site and species vector arrows were deleted for clarity. Crosses (+) indicate binary variables used to detect treatment effects. Species codes are defined in Table 2; environmental variables are defined in Table 3.

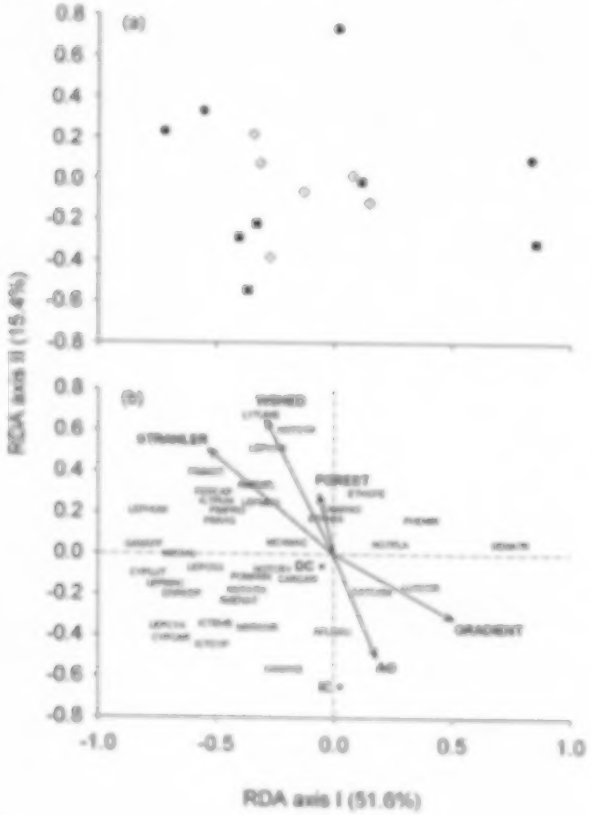
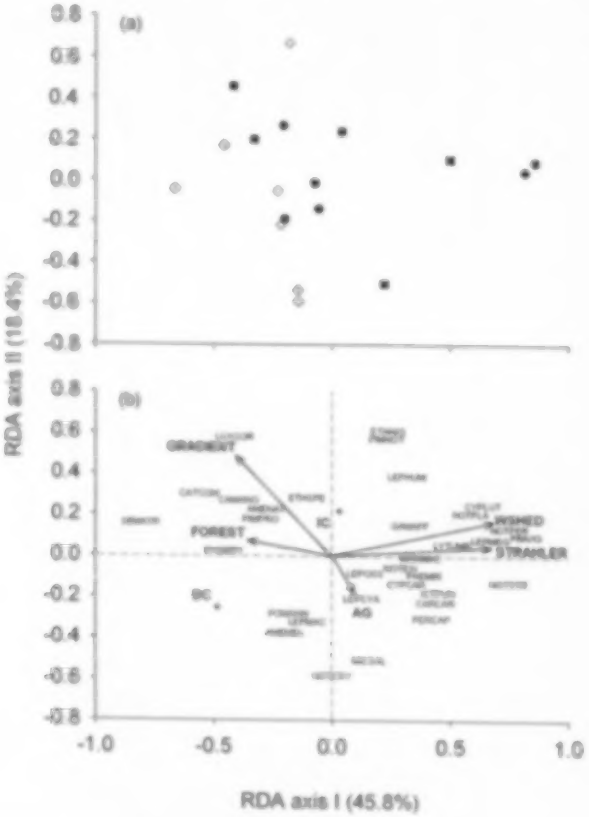


Fig. 5. Association of fish species environmental variables and connectivity type (DC, directly connected; IC, indirectly connected) (*b*) at sites located halfway up the perennially wetted length of a stream from a redundancy analysis (RDA). Site scores are plotted in (*a*): ◇, directly connected sites; ■, indirectly connected sites; ●, control sites. Site and species vector arrows were deleted for clarity. Crosses (+) indicate binary variables used to detect treatment effects. Species codes are defined in Table 2; environmental variables are defined in Table 3.



sites were evenly misclassified as directly connected or control sites 40% of the time. Three species were entered into the analysis from the stepwise procedure: sand shiner, red shiner, and bluntnose minnow. Discriminant function 1 separated the connectivity categories based on high abundances of red shiner at indirectly connected sites, sand shiner at control sites, and bluntnose minnow at directly connected sites. Group means in discriminant functions 1 and 2 were significantly different from one another (Wilks' lambda = 0.11, $P < 0.001$).

In contrast to results of the RDA, middle sites were 87.0% correctly assigned to connectivity categories using the DFA cross-validation approach, suggesting subtle differences in assemblage structure among the stream categories. In this case, indirectly connected sites were classified correctly 100% of the time, whereas directly connected and control sites were grouped correctly 75.0% and 88.9% of the time, respectively. Species entered into the model for middle sites were redfin shiner, yellow bullhead (*Ameiurus natalis*), and central stoneroller. Discriminant function 1 separated the reservoir connectivity groups based on high abundances of redfin shiner at control sites, yellow bullhead at indirectly connected sites, and central stoneroller at directly connected sites. Group means of discriminant functions 1 and 2 were significantly different from one another (Wilks' lambda = 0.13, $P < 0.001$).

Effects of reservoir connectivity within streams

A total of 8369 individuals representing 26 species were captured in the 22 pools in Baldwin and Mill creeks, and species richness ranged from 6 to 18 across pools. Minnows numerically dominated the collections, as southern redbelly dace (relative abundance 27.1%), central stoneroller (25.2%), and common shiner (18.8%) were the most common species collected.

Discriminant function analysis revealed differences in physical habitat parameters between the two streams. Sam-

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ple sites from the two streams were correctly classified based on physical habitat 91% of the time (Wilks' lambda = 0.321, $P < 0.001$). Compared with Mill Creek, Baldwin Creek was a smaller stream, containing smaller, shallower pools, with a higher proportion of canopy cover. Based on these results, we analyzed each stream separately.

PCA I of physical habitat was significantly correlated with distance from the reservoir for both Baldwin Creek ($r = 0.72$, $P = 0.009$) and Mill Creek ($r = 0.66$, $P = 0.04$). Regardless, fish assemblage structure did not vary across sites with increasing reservoir distance based on a consensus of several analyses. Mean Jaccard's index of similarity based on presence or absence of fish species between the site nearest the confluence and all other sites was 0.50 (SE = 0.04) for Baldwin Creek and showed no pattern with reservoir distance (Fig. 6). Similarly, mean Jaccard's index of similarity for Mill Creek was 0.61 (SE = 0.04) and did not show a pattern with reservoir distance (Fig. 6). When we considered patterns in species abundances based on percent similarity, there also was no correlation with reservoir distance. Mean PSI values (± SE) across sites were 0.50 ± 0.04 for Baldwin Creek (Fig. 6) and 0.64 ± 0.06 for Mill Creek (Fig. 6). Further, when we partitioned variation in the data set into that explained by physical habitat versus reservoir distance using RDA for each stream, we found that axes I and II of the partial RDA using physical habitat variables as covariates were not significantly different from random for both streams (Ps > 0.12). This suggests that variability in fish assemblage structure in these streams was better explained by physical habitat parameters than by reservoir proximity.

In contrast to the above patterns of assemblage structure, when evaluating reservoir species abundance (total number of individual reservoir species collected in each pool) in Baldwin Creek, there was a rapid decline to zero as reservoir distance increased. However, in Mill Creek, reservoir species were present, but in low abundance, in pools throughout the stream (Fig. 7). Using stepwise procedure to select variables in a multiple regression model using both streams, we found that organic matter, pool volume, percent canopy cover, and maximum depth explained 79% of the variation in reservoir species abundance in pools within our study area ($P < 0.001$; Table 4).

Discussion

Our data suggest that the influence of reservoir connectivity on stream fish assemblage structure was highly localized. We found that total, nonnative, and reservoir species richness were all higher at reservoir confluences than at sites farther upstream. Although this pattern may partly be explained by within-stream longitudinal processes, many of the species that make up the difference in richness between confluence and middle sites migrate to confluence sites from the reservoir. In streams directly flowing into reservoirs, there also was a trend for a greater difference in the total species richness between confluence and middle sites than in other stream types. This follows our prediction that isolation would result in species extirpations in these streams and that reservoir confluences would have greater numbers of nonnative and reservoir species. Was the paucity of species at upstream sites in these isolated streams due to reservoir effects? At least two species have been extirpated from streams directly connected to our study reservoirs, Topeka shiner (*Notropis topeka*) and carmine shiner (*Notropis percobromus*) (Minckley and Cross 1959; Cross and Collins 1995). Loss of refugia from stochastic abiotic conditions combined with downstream habitat changes from reservoir construction is cited as the primary cause of decline in these species (Cross 1967; Cross and Collins 1995). These altered conditions in directly connected streams could explain the lower richness observed in the middle sites.

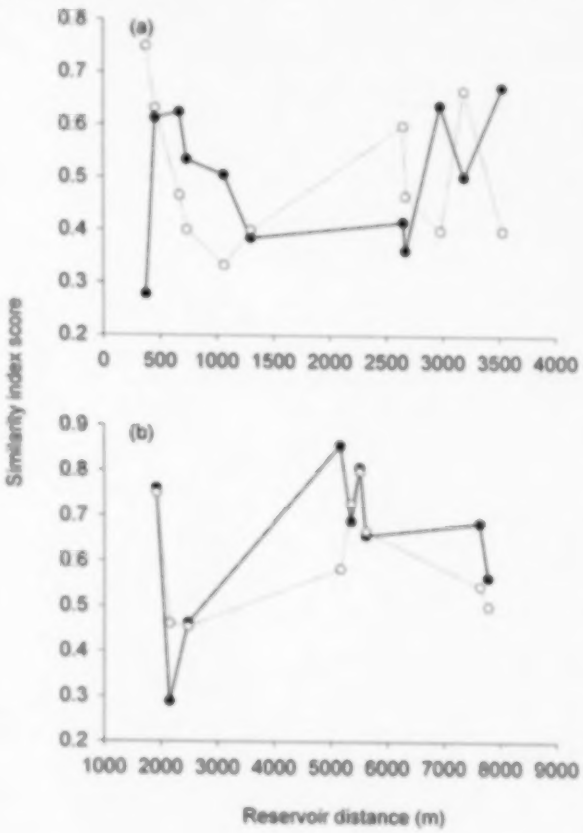

Fig. 6. Similarity of pool fish assemblages in (*a*) Baldwin and (*b*) Mill creeks versus distance from a reservoir. Assemblage similarity was compared between each pool and the pool closest to the reservoir using percent similarity (●) and Jaccard's (○) indices.

The observed differences in assemblage structure between confluence and middle sites were not unexpected, as longitudinal processes can influence assemblage structure in lotic systems (Horwitz 1978; Schlosser 1987). However, assemblages at sites near confluences also are influenced by an "edge" effect, in addition to longitudinal processes. This was illustrated by the co-occurrence of large river or reservoir and small stream species at these sites. Thus, assemblage structure at confluences is likely influenced by a combination of upstream longitudinal processes and emigration from downstream reservoirs.

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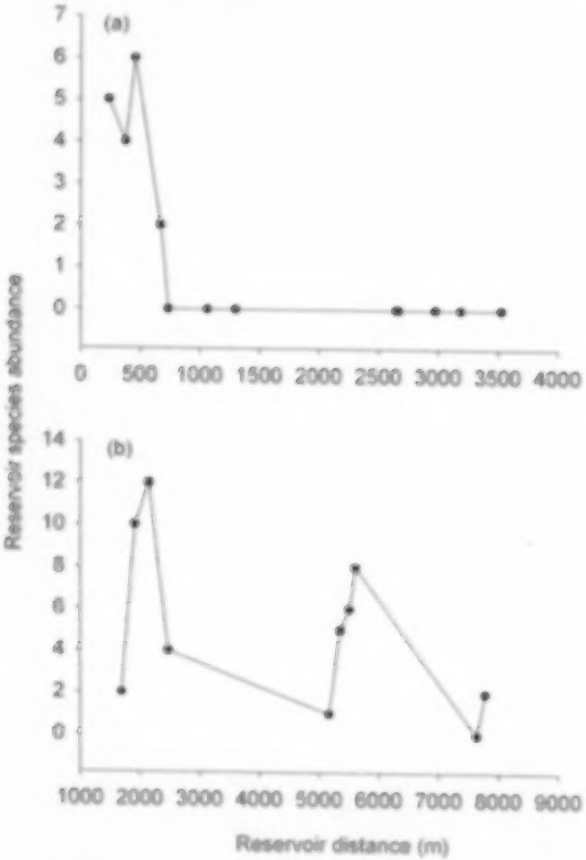
Table 4. Results from a stepwise multiple regression analysis of the influence of physical habitat features on the abundance of reservoir species in pools in two Flint Hills streams directly connected to a reservoir.

Source	df	F value	P value	R^2	Variable	df	Standardized parameter estimate	t	P value
Model	4	15.61	<0.001	0.786	Organic matter	1	0.411	3.37	0.004
Error	17				Pool volume	1	–0.537	–3.93	0.001
Total	21				Canopy cover	1	–0.380	–3.13	0.006
					Maximum depth	1	–0.307	–2.34	0.032

Fig. 7. Abundance (number collected per pool) of reservoir species collected in pools in (*a*) Baldwin and (*b*) Mill creeks versus distance from a reservoir (m).



Ordination of fish assemblages at confluence sites revealed differences in structure among connectivity types. Separation in sites based on assemblage structure was apparent among control streams and the other two connectivity types. Whereas piscivorous reservoir species (e.g., largemouth bass (*Micropterus salmoides*), white bass, and white crappie (*Pomoxis annularis*)) were closely associated with directly and indirectly connected streams, confluence sites in control streams were associated with native species (e.g., sand shiner, redfin shiner, and black bullhead (*Ameiurus melas*)). One confounding factor was the disproportionate coverage of agriculture in the catchments of indirectly connected streams, which could have influenced assemblage structure independent of reservoir connectivity. Classification of sites into connectivity groups was partially successful, further indicating differences in fish assemblage structure among connectivity types. Indirectly connected confluence streams were evenly misclassified between directly connected and indirectly connected groups, indicating a possible gradient of connectivity effects between the three categories. The abundance of sand shiners was a strong predictor of connectivity type at confluence sites; directly and indirectly connected streams had very low abundances of this typically common species as compared with control streams. Low abundance of sand shiners in these reservoir-influenced sites may be a cause for concern, as other minnows with similar life history traits (e.g., western silvery minnow (*Hybognathus argyritis*), plains minnow (*H. placitus*), and peppered chub (*Macrohybopsis tetranema*)) have drastically declined in incidence and abundance upstream of reservoirs in these systems (Cross and Collins 1995; Gido et al. 2002*b*).

Assemblage structure at middle sites was weakly linked to connectivity, although directly and indirectly connected sites generally had higher abundances of bluegill (*Lepomis macrochirus*), largemouth bass, and white crappie than control sites. The presence of these species, however, could be influenced by numerous small impoundments in directly and indirectly connected watersheds. Overall, most variation in fish assemblage structure in middle sites was not related to connectivity with a reservoir. Rather, assemblage structure at middle sites was primarily driven by catchment area, stream size, and gradient. Nevertheless, DFA accurately predicted if a site was a control stream based on high redfin shiner abundance, suggesting a potentially subtle effect of reservoir connectivity on assemblage structure. Although currently not a species of concern, redfin shiner commonly occurs with other species that have been cited as being imperiled in Kansas, including Topeka shiner and common shiner (*Luxilus cornutus*) (Haslouer et al. 2005). Low incidence of redfin shiner at upstream sites in directly and indirectly connected streams may stem from influences of downstream reservoirs or habitat degradation resulting from agricultural practices within the watershed.

Within-stream patterns in fish assemblage structure were also weakly linked to proximity to the reservoir. Abundance of reservoir species in pools along Mill Creek did not vary with distance from the reservoir, whereas the abundance of these species declined in pools furthest from the reservoir in Baldwin Creek. Mill Creek is a larger stream than Baldwin Creek (4th vs. 3rd order), with deeper pools and more complex habitat, thus the observed pattern may be related to more available suitable habitat for reservoir species in Mill Creek. However, patterns in assemblage structure in Baldwin Creek are influenced by recent hydrologic events. Spe-

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cifically, five of the seven upstream-most pools sampled in Baldwin Creek were completely dried during 2003 (H. Klaassen, Leonardville, Kansas, personal communication). Desiccation of habitat may have forced fish occupying this area downstream to more suitable habitat (compensatory movement; sensu Winston et al. 1991). High abundances of more typical "headwater" species (e.g., southern redbelly dace and central stoneroller) in pools near the confluence and relatively low species richness and (or) abundance in upstream pools may reflect a failure of the headwater species to recolonize upstream.

Downstream compensatory movement of fishes into pools near the reservoir places them at higher risk of predation because of the presence of piscivorous reservoir species. Thus, reservoirs may act as barriers simply because of the presence of predators. Predation barriers are known to occur among tributary streams connected to main-stem rivers that are occupied by predators (e.g., Fraser et al. 1995). Nevertheless, it was interesting to note that there was a general increase in species richness at stream–reservoir interfaces because of the co-occurrence of native stream fishes and predators. Quantification of competitive and predator–prey interactions among reservoir and native species at the stream–reservoir interface is needed to determine the consequences of connectivity to these habitats.

The exact mechanism limiting reservoir species occurrences in upstream reaches was unclear. In Baldwin and Mill creeks, we found that reservoir species abundance was associated with large, deep pools with relatively high turbidity and a low proportion of canopy cover. These conditions were typical of pools near reservoirs, where large pools result from longitudinal catchment geomorphological processes, and canopy cover has been reduced by numerous inundations by the reservoir in high-water years. Higher turbidity (as indicated by relatively high amount of organic matter within these pools) may result from a combination of upstream inputs and silt deposition from prior inundation during the spring. Lack of the above-mentioned conditions, as well as the more stochastic nature of environmental conditions upstream, may prevent reservoir species from colonizing upstream pools in this study area. Thus, the lack of reservoir species at upstream sites may be primarily attributed to habitat limitations, as appeared to be the case in Mill Creek where reservoirs species occurred throughout the 10 study pools between the middle site and confluence site. Alternatively, there may be physical barriers that limit the spread of reservoir species upstream. In many Flint Hills streams, there are small cascading waterfalls (up to 1 m) and road culverts that may limit the movement of fishes upstream. Clearly, as a fish travels further from a reservoir, the likelihood of encountering a barrier increases.

In conclusion, overall assemblage structure observed among streams in the Flint Hills region showed a very localized effect (1–10 km) of reservoirs on stream fish assemblages. We found higher abundances of nonnative and reservoir species in close proximity to reservoirs; however, their abundance quickly declined as distance from a reservoir increased, with the exception of Mill Creek. These observations at moderate and small spatial scales agree with previous patterns observed at large spatial scales in streams upstream of Kansas reservoirs (Falke and Gido 2006).

Understanding the influences of stream connectivity to reservoirs has several implications for conservation of native fishes in the Great Plains. First, streams isolated by reservoirs may not be suitable targets for conservation (e.g., land acquisition or restocking) if downstream compensatory movement of fishes, when upstream conditions become unsuitable, places them at higher risk of competition or predation. This is particularly apparent given our finding that downstream pools had higher abundances of nonnative and reservoir species. Second, although indirectly connected streams would seem to be better choices for conservation, streams in this region also are more heavily impacted by agriculture than streams of other connectivity types. With this in mind, careful selection of catchments using landscape-scale analysis (e.g., Gido et al. 2006) could target indirectly connected streams with relatively low proportions of agriculture in their catchments.

Choosing streams for conservation efforts is critically needed in the Great Plains, as there are a large number of imperiled fishes (Cross and Moss 1987; Fausch and Bestgen 1997; Haslouer et al. 2005) and the majority of streams within Kansas are impacted by human activities. Although our data suggest a localized effect of reservoirs on stream fish assemblages, it is important to note that our control streams were not free of human alteration (e.g., changes in water chemistry) and generally did not represent pristine fish assemblages. Thus, if considerable homogenization of the regional fish fauna has occurred (Rahel 2000; Falke and Gido 2006), our evaluation of the effects of connectivity are likely weakened by our lack of true "control" streams. Conservation of streams not influenced by reservoirs may be critical, as these streams were occupied by several species (e.g., sand shiner and redfin shiner) that were absent or rare in streams connected to reservoirs. However, because reservoirs are a dominant feature of the landscape, it is also important to recognize that many other native species can persist in streams connected to reservoirs, and these habitats should not be overlooked for conservation actions.

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Life history correlates of density-dependent recruitment in marine fishes

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Abstract: Understanding the relationships among life history traits, density dependence, and population dynamics is a central goal in ecology. It is also vital if we are to predict how populations respond to and recover from exploitation. We used data for 54 stocks of commercially exploited fish species to examine relationships between maximum annual recruitment at low stock size and the density dependence of recruitment at high stock size. We then related these recruitment measures to life history. At low stock sizes, stocks with high maximum recruitment (maximum spawners per spawner) showed the weakest density dependence of recruitment at high stock sizes. Spawning biomass per recruit in the absence of fishing ($SPR_{F=0}$) showed a strong positive correlation with both maximum spawners per spawner and the strength of density dependence. Stocks with high $SPR_{F=0}$ were typically large-bodied, slow-growing, late-maturing, and highly fecund with long generation times. These stocks produced low numbers of recruits each year, but survived to breed repeatedly and had strong density dependence of recruitment. In contrast, small-bodied, early-maturing fish had high annual recruitment and weak density dependence. These results place species on a continuum from "highly reproductive" to "survivors". But we also demonstrate that density dependence is an important feature of the population biology of survivors.

Résumé : La compréhension des relations entre les caractéristiques démographiques, la dépendance de la densité et la dynamique de population est un des principaux objectifs de l'écologie. Elle est aussi essentielle pour la prédiction des réactions des populations à l'exploitation et de leur récupération subséquente. Nous utilisons des données provenant de 54 stocks de poissons exploités commercialement afin d'examiner les relations entre le recrutement maximum annuel lorsque les stocks sont bas et la dépendance du recrutement de la densité lorsque les stocks sont élevés. Nous relions ensuite ces estimations du recrutement à la démographie. Lorsque les stocks sont bas, les stocks qui ont un fort recrutement maximum (nombre maximum de reproducteurs par reproducteur) montrent la dépendance de la densité de leur recrutement la plus faible lorsque les stocks sont élevés. La biomasse des reproducteurs par recrue en absence de pêche ($SPR_{F=0}$) est en forte corrélation positive à la fois avec le nombre maximum de reproducteurs par reproducteur et avec l'importance de la dépendance de la densité. Les stocks avec un $SPR_{F=0}$ élevé ont typiquement un grand corps, une croissance lente, une maturation tardive, une forte fécondité et une durée de génération importante. Ces stocks produisent un petit nombre de recrues chaque année, mais ils survivent assez longtemps pour se reproduire plusieurs fois et leur recrutement montre une forte dépendance de la densité. En revanche, les poissons à corps plus petit et à maturation précoce ont un recrutement annuel élevé et une faible dépendance de la densité. Ces résultats permettent de placer les espèces le long d'un continuum allant des « reproducteurs prolifiques » aux « survivants ». Nous démontrons aussi, cependant, que la dépendance de la densité est une caractéristique importante de la biologie de population des survivants.

[Traduit par la Rédaction]

Introduction

Life histories and density dependence are pivotal to our understanding of population dynamics (Roff 1992; Stearns 1992; Tuljapurkar and Caswell 1997). Species with high intrinsic rates of population increase (r) are expected to have a high capacity to recover from overexploitation or from an environmental shock that reduces the population (Myers et al. 1997; Hutchings and Reynolds 2004). However, population growth rates are also determined by density dependence

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and environmental stochasticity. We need to understand the interplay among these processes to predict the ability of populations to withstand human impacts, such as fishing. Unfortunately, both r and the strength of density dependence are difficult to measure in wild populations. This has led to a search for simple aspects of the biology of species that can be used to predict these key parameters, and hence population dynamics, at both low and high population sizes.

Life history theory offers a promising framework for building bridges between demography and fundamental aspects of species biology. There is now a large body of empirical evidence supporting predictions of trade-offs between life history components that underpin adaptations for maximizing individual fitness (reviewed in Stearns 1992; Charnov 1993; Roff 2002). For example, previous studies of commercially exploited marine fishes have identified life history traits, such as body size and age at maturity, that predict maximum recruitment at low population size (Dennery et al. 2002) and abundance trends in exploited species (Jennings et al. 1998; Reynolds et al. 2005; Hutchings and Reynolds 2004). To date, no study has examined whether such life history traits are correlated with reductions in recruit survival with increasing population size, otherwise known as density-dependent recruitment or compensation.

At high population sizes, density-dependent processes that reduce the number of recruits produced per spawner are thought to result from competition for habitats and food, leading to limits on population sizes (Rose et al. 2001; Myers 2002). This density dependence results in a less than proportional increase in recruitment with population size, giving a population some capacity to compensate for the effects of exploitation (Cushing 1975) and also giving it some assimilative capacity to resist the effects of pollution, poor environmental conditions, or other environmental shocks (Grant 1998). There is evidence that life history traits may influence the degree of density-dependent mortality because species that reach a stable equilibrium population size tend to be slow growing, late maturing, and have high early survival (Stearns 1992; Roff 2002). However the reasons behind these relationships have been the subject of extensive debate. Pianka (1970) suggested that selection pressures on some species favour rapid population growth, whereas those on other species favour competitive ability. Stearns (1976) presented bet-hedging as an alternative conceptual framework, in which longer-lived adults maximize individual fitness in a variable environment by breeding many times, rather than having one or a few large bursts of reproduction, as is typical of fast-growing or semelparous species (reviewed by Winemiller 2005). Debates of these issues have suffered from a paucity of evidence on the significance of density dependence in wild populations and a failure of a number of studies to find any trade-off between competitive ability at high densities and population growth rate at low densities (e.g., Luckinbill 1978; Velicer and Lenski 1999).

The aim of this study is to establish whether there is a relationship between maximum recruitment at low population sizes and the strength of the density-dependent recruitment (or compensatory reserve), as indicated by a decline in recruits per spawner at high population sizes. We also aim to identify whether any life history traits are correlated with the strength of density dependence at high population sizes for a wide range of fish stocks. Ultimately, we hope to use life history as an a priori predictor of density-dependent relationships for data-poor populations.

Materials and methods

Data sources

We collated age-structured life history information and time series of adult and recruit abundances for stocks of commercially exploited marine fishes in the northeast Atlantic. These data were published by regional Working Groups, whose assessments are available from the International Council for the Exploration of the Sea (ICES; http://www.ices.dk/iceswork/workinggroups.asp). ICES stock assessments use virtual population analysis of commercial catch-at-age data to estimate annual spawning stock biomass and age-specific vital rates and recruit abundance (Pope 1972; Darby and Flatman 1994). We derived life history measures from the most recent 5-year mean values of weight, maturity, and natural mortality at age. Fecundity was derived from published weight–fecundity or length–fecundity relationships. Spawner–recruit relationships were calculated only for stocks with a spawner and recruit abundance time series of at least 15 years and when the range of spawning biomass was at least 50% of the maximum observed spawning biomass. This criterion reduced the data set to 54 stocks from a possible 63. The median length of time series was 29 years, with a range from 15 to 93 years. Typically, the minimum observed spawning stock biomasses were 74% (±2.2% standard error, SE) lower than the maximum observed biomass.

Life history parameters

Asymptotic weight (W_∞), referred to here as maximum weight, and body growth rate (κ) were estimated from the von Bertalanffy growth equation:

$$(1) \qquad W(i) = W_\infty[1 - e^{-\kappa(i - i_0)}]^b$$

where $W(i)$ is weight at age i, κ is body growth rate, i_0 is the age at hatching, and b is the exponent from the length–weight relationship ($W = aL^b$). In the absence of stock assessment values of b (39 of 54 stocks), regional or species means were taken from FishBase (Froese and Pauly 2004). Weight-at-age data were based on a 5-year mean of catch weights from the most recent stock assessment. We only included age classes fully selected by the fishery because mean weights at age for younger age classes could be biased towards the larger individuals more likely to be caught. Although this excludes some age classes, the von Bertalanffy parameters were estimated over a wide range of weights. Typically, the minimum observed body weights were 84% (±1.5% SE) lower than the maximum body weight. For parameter estimation, a nonlinear least squares technique (see Quinn and Deriso 1999) was used to fit both an additive and a multiplicative error-structured model for eq. 1, for which the multiplicative model was first converted to its natural logarithm. Starting parameters were W_∞ = maximum observed weight, $\kappa = 0.2$, and $i_0 = 0$. We used estimates of W_∞ and κ from the model with the lowest sums of squares and narrowest confidence intervals.

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The age at 50% maturity (T_{mat}) was calculated from the logistic function where the rate of change is a parabolic function of age:

$$(2)\qquad \mathrm{Mat}(i) = \frac{1}{1+e^{-\theta(i-T_{mat})}} \qquad (\theta, T_{mat} > 0)$$

where Mat(i) is the proportion mature at age i, θ represents the curvature of the logistic curve, and T_{mat} is the age at the inflection point. Parameters were estimated using a nonlinear least squares data fitting by the Gauss–Newton method. The initial starting value for T_{mat} was taken from the first age class in which more than 50% of individuals were observed to be mature.

Fecundity at the age at 50% maturity (Fec_{mat}) was calculated from the linear interpolation of log-transformed mean fecundity at age. Mean fecundity at age was derived from weight-at-age data taken from stock assessments and published weight–fecundity and length–fecundity relationships.

We also used two life history measures that incorporated the combined elements of survival, reproduction, and body growth rate. Generation time (G) is the mean time between reproduction of the parent generation and reproduction of its own offspring and is calculated as

$$(3)\qquad G = \frac{\sum x l_x m_x}{\sum l_x m_x}$$

where x is the age class, l_x is the probability of survival, and m_x is the mean fecundity. Spawners per recruit ($\mathrm{SPR}_{F=0}$) is the cumulative spawning biomass (kg) produced by a recruit over the course of its lifetime in the absence of fishing mortality (Gabriel et al. 1989):

$$(4)\qquad \mathrm{SPR}_{F=0} = \sum_{i}^{i_{max}} N_i e^{-(M_i(i-i_{rec})+i_{rec})} W_i \mathrm{Mat}_i$$

where $N_i = 1$ is the recruit present in the first age class, W_i is weight (kg) at age i, Mat_i is the proportion mature at age i, M_i is natural mortality at age i, and i_{rec} is the age at recruitment. The term i_{rec} is included to ensure that the calculation of $\mathrm{SPR}_{F=0}$ starts from the same age class for all stocks, otherwise stocks whose recruits are counted in older age classes would have disproportionately high values of $\mathrm{SPR}_{F=0}$. This calculation makes the simplifying assumption that fecundity is proportional to body weight after adjusting for the fraction of fish in each age class that are mature. The same assumption is made in most stock assessments. Life history parameters and measures are summarized for each stock (Appendix Table A1).

Estimating spawner–recruit parameters

Within a fisheries context, recruits are juvenile fish of a given age that become vulnerable to fishing gear used in research surveys. The age of this vulnerability varies among species (Appendix Table A2). Various models can be used to describe the form of the density-dependent relationship between spawner biomass and the numbers of recruits (see Hilborn and Walters 1992; Quinn and Deriso 1999). We used the Ricker (1954) and hockey stick (Barrowman and Myers 2000) models because together they capture a wide range of spawner–recruit relationships, and their statistical fit was more robust across a range of stocks than for a more complex, three-parameter model (e.g., Shepherd 1982). Both models assume an upper limit to recruitment. The Ricker model has the form

$$(5)\qquad R_t = \alpha S_t e^{-\beta S_t + \varepsilon_t} \qquad (\alpha, \beta > 0, \varepsilon)$$

where the number of recruits R_t is a function of S_t, where S is the spawner biomass at time $t - i_{rec}$, α is the slope at the origin, and β governs the population size at which density dependence occurs. We introduce variation in recruitment after density-dependent regulation, where ε_t is a normal recruitment variation with a mean of 0 and variance σ^2. The parameter α is the maximum annual recruit production, and the product of β and S_t is density-dependent recruit mortality. The hockey stick model has the form

$$(6)\qquad R_t = \alpha \min(S, S^*, \varepsilon) = \begin{cases} \alpha S_t e^{\varepsilon_t} & \text{if} \quad S_t < S^* \\ \alpha S^* e^{\varepsilon_t} & \text{if} \quad S_t \geq S^* \end{cases}$$

where α is the linear slope of a bisected line up to the point S^*, which is the spawner biomass beyond which there is a constant number of recruits for further increases in stock size, and ε_t is the normal recruitment variation with mean of 0 and variance σ^2.

Ricker and hockey stick parameters were estimated using maximum likelihood procedures. We used a lognormal error distribution for the likelihood function:

$$(7)\qquad \ell(R|\hat{\sigma}) = -\frac{n}{2}\log_e\left\{\frac{2\pi}{n}\sum[\log_e R_t - \log_e f(S_t)]^2\right\} - \sum \log_e R_t - \frac{n}{2}$$

where R_t is the number of recruits in each year, the estimated $\hat{\sigma}$ is the standard deviation of recruit variation, n is the length of the time series, and $f(S_t)$ is the number of recruits predicted from spawning stock biomass (SSB) by either the Ricker or hockey stick models above. Starting parameters for the Ricker model were estimated from a least squares regression of the linear form $\log_e(R/S) = \log_e(\text{intercept}) - (\text{slope})S$, where $\alpha = \exp(\text{intercept})$ and $\beta = -\text{slope}$ (Quinn and Deriso 1999). Starting parameters for the hockey stick model were $\alpha = 1$ and $S^* =$ spawning stock biomass at median recruitment. Evaluation of the maximum likelihood values indicated that the Ricker model provided a better fit to the spawner–recruit data than did the hockey stick model in 32 of the 54 stocks. The hockey stick failed when the turning point S^* could not be reconstructed. Spawner–recruit parameters, standard deviations based on bootstrap analysis, and model fits are presented for each stock (Appendix Table A2).

Spawner–recruit parameter estimation may be influenced by serial correlation in the time series, whereby annual spawner–recruit data lack independence because years of strong recruitment may have a positive or negative effect on future spawning biomass and recruitment (Walters 1985). A first-order autoregressive model of recruitment did not improve the model fit (for all 54 stocks: $\chi^2 < 2.06$; df = 1; $p > 0.15$). Before including a wide range of potential lagged

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effects, further work is required to interpret how serial correlation influences parameter estimates and density-related processes.

Calculation of the equilibrium spawning stock biomass

The mean equilibrium for the unexploited spawning stock biomass ($SSB_{F=0}$) was calculated using an age-structured, stochastic population model without fishing mortality. Annual recruitment variation was lognormally distributed around the fitted spawner–recruit relationship. The numbers in each age class i were calculated as

$$(8)\quad N_{(i+1,t+1)} = N_{(i,t)}\,e^{-M} \quad \text{for } i = \text{age at recruitment to } i_{\max} - 1$$

$$N_{(i_{\max},t)} = N_{(i_{\max},t)}\,e^{-M} + N_{(i_{\max}-1,t)}\,e^{-M}$$

where N_i is the number of individuals in each age class at time t, and M is the instantaneous rate of natural mortality; $i_{\max}$ is the age at which we assume demographic parameters no longer change with age, so the age class $i_{\max}$ denotes all individuals of age $i_{\max}$ and older. The age class aggregation is the plus group described in stock assessments and typically contributed between 2% and 9% of the spawning biomass. In each yearly time step, the total SSB was the summed weight of all reproductive males and females in the stock.

$$(9)\quad \mathrm{SSB} = \sum_{i}^{i_{\max}} N_i W_i \mathrm{Mat}_i$$

The number of individuals entering the stock as new recruits is a function of SSB (eq. 9) and either the Ricker or hockey stick models of recruitment (eqs. 5 and 6). $SSB_{F=0}$ was calculated as the mean biomass over 1000 time steps after equilibrium had been reached. We used both models of recruitment to ensure that results were not merely a function of the choice of spawner–recruit relationship.

Standardized measures of density-independent and density-dependent recruitment

Maximum annual recruitment per spawner (α) is described by the slope at the origin from either the Ricker or hockey stick models (eqs. 5 and 6). However, α is not directly comparable across stocks with different life histories. Individuals with short reproductive life spans must have higher annual recruitment to replace themselves, whereas long-lived individuals spawn over many years and can replace themselves at lower levels of annual recruitment. The standardized, density-independent measure of α accounts for differences in an individual's lifetime recruit production, which is a function of their expected lifetime spawning biomass discounted for repeat spawning over their lifespan (Myers et al. 1997, 1999). We first calculate the maximum recruits per recruit at low spawner abundance ($\hat{\alpha}$; the product of α and $SPR_{F=0}$) (Gabriel et al. 1989; see eq. 4 above). The final standardized unit for comparison across stocks, maximum spawners per spawner ($\tilde{\alpha}$), is defined as the average number of adult spawners that are produced annually per spawner at low spawner abundance. If p_s is the annual adult survival, such that $p_s = e^{-M}$, then $\hat{\alpha} = \sum_{i=0}^{\infty} p_s^i \tilde{\alpha}$. The sum of this geometric series (eq. 10*a*) can be rearranged to give $\tilde{\alpha}$ (Myers et al. 1997, 1999).

$$(10a)\quad \hat{\alpha} = \tilde{\alpha}/(1 - p_s)$$

$$(10b)\quad \tilde{\alpha} = \hat{\alpha}(1 - p_s) \qquad \text{where } \hat{\alpha} = \alpha\,\mathrm{SPR}_{F=0}$$

A measure of negative density-dependent recruit mortality reveals a less than proportional increase in recruit survival with increasing spawning stock biomass. Stocks that show a strong reduction in recruit survival have the greatest compensatory capacity to buffer against increases in adult mortality. Goodyear (1977) developed an index of this compensatory capacity, the compensation ratio (CR), to illustrate the reduction in compensatory reserve with increased fishing (decreasing spawning biomass). CR is used here as a standardized measure of density-dependent recruitment to compare across stocks and is calculated as the ratio

Fig. 1. Graphic representation of the compensation ratio (CR) for (*a*) Ricker and (*b*) hockey stick spawner–recruit models. When spawning stock biomass is at unexploited levels ($SSB_{F=0}$), both stock 1 and stock 2 have lower recruit survival per spawner (*R*/*S*) compared with their maximum recruit survival at low stock sizes (α; dashed line). The closer the gradient of the stock replacement line is to the gradient of α, the weaker the effect that density has on *R*. So stock 2 has a higher CR (eq. 11) and is exposed to stronger density-dependent recruit mortality than stock 1.

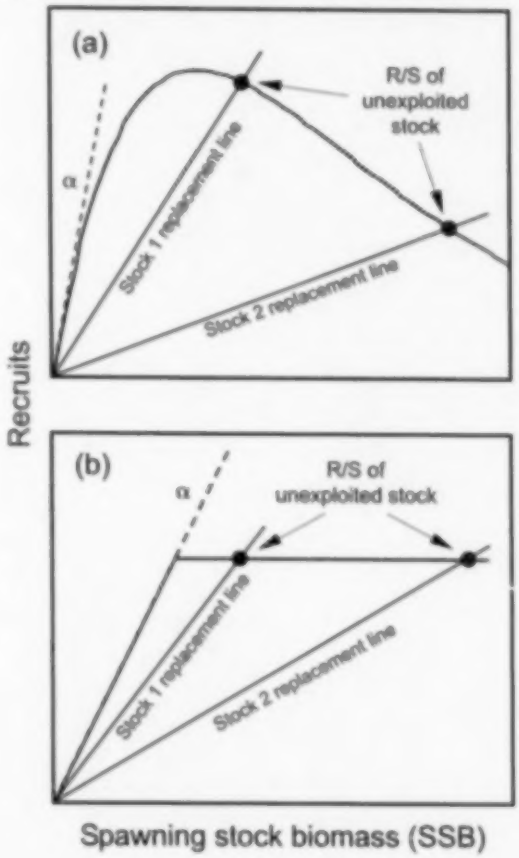

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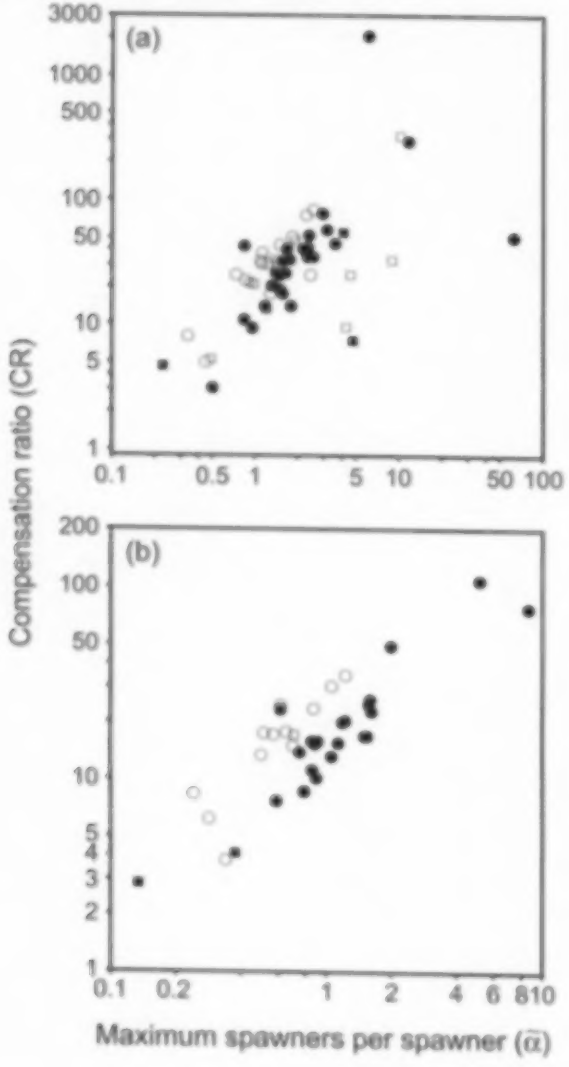
Fig. 2. Correlation between $\log_e$ maximum spawners per spawner ($\tilde{\alpha}$) and $\log_e$ compensation ratio (CR) derived for stocks based on (*a*) Ricker, and (*b*) hockey stick spawner–recruit models. High values of CR indicate strong density-dependent recruitment. □, Clupeiformes; ●, Gadiformes; ■, Perciformes; ○, Pleuronectiformes.



of maximum recruit survival, taken as the slope at the origin (α) or a spawner–recruit curve, and $SSB_{F=0}$ (eq. 11) (Fig. 1).

$$(11)\quad CR = \frac{\alpha}{\text{Recruit survival at } SSB_{F=0}}$$

A compensation ratio of one indicates no change in recruit mortality over the whole range of spawning biomass; higher values indicate strong decline in recruit survival. Values for $\tilde{\alpha}$, $SSB_{F=0}$, and CR are presented in Appendix Table A3.

Results

CR was strongest in stocks with high maximum spawners per spawner ($\tilde{\alpha}$) (Ricker: Pearson's $r = 0.62$, $n = 54$, $p < 0.001$; hockey stick: $r = 0.85$, $n = 36$, $p < 0.001$; Fig. 2). This correlation did not depend on the form of the spawner–recruit model, and estimates of $\tilde{\alpha}$ and CR were similar for the dome-shaped Ricker and plateau-shaped hockey stick models ($\tilde{\alpha}$: $r = 0.88$, $n = 36$, $p < 0.001$; CR: $r = 0.88$, $n = 36$, $p < 0.001$). The pattern of $\tilde{\alpha}$ versus CR was also consistent among stocks and species within Gadiformes and Pleuronectiformes, the two orders with sufficient data points for comparison (Fig. 2). The hockey stick correlation between $\tilde{\alpha}$ and CR was stronger than that with the Ricker model because 18 of the 54 stocks did not fit the hockey stick recruitment model. When the 54 stocks were split into two groups (those that did fit a hockey stick model ($n = 36$) and those that did not ($n = 18$)), we found that the hockey stick did not fit stocks characterized by high values of Ricker's α (Ricker mean $\log_e\alpha \pm 1$ SE: hockey stick did fit = 1.04 ± 0.15; hockey stick did not fit = 4.00 ± 0.40; $t_{52} = 6.86$; $p < 0.001$). Stocks that did not fit the hockey stick model also had low values of $SPR_{F=0}$ (mean $\log_e SPR_{F=0} \pm 1$ SE: hockey stick did fit = 1.28 ± 0.17; hockey stick did not fit = -1.20 ± 0.44; $t_{52} = -5.29$; $p < 0.001$). However, these same stocks were not characterized by weak density dependence (Ricker mean $\log_e$ CR ± 1 SE: hockey stick did fit = 3.50 ± 0.18; hockey stick did not fit = 3.10 ± 0.25; $t_{52} = -1.34$; $p = 0.188$).

One explanation for the strong positive correlation between $\tilde{\alpha}$ and CR might be that stocks with high α could achieve maximum recruitment at lower spawning stock sizes, and so for a given mean unexploited SSB they would show a stronger degree of density-dependent recruitment. However, this is not the correct interpretation because, with one exception, α showed weak or no association with $\tilde{\alpha}$ (Ricker: $r = 0.36$, $n = 54$, $p = 0.007$; hockey stick: $r = -0.08$, $n = 36$, $p = 0.625$; Figs. 3*a*, 3*b*) or with CR (Ricker: $r = -0.12$, $n = 54$, $p = 0.375$; hockey stick: $r = -0.052$ $n = 36$, $p = 0.907$; Figs. 3*c*, 3*d*).

The composite life history measure ($SPR_{F=0}$) proved to be the best single predictor of both α and CR (Fig. 4). Stocks with high $SPR_{F=0}$ had the lowest α (Ricker: $\log_e \alpha = 2.44 - 0.91\log_e SPR_{F=0}$, $r^2 = 0.76$, $F_{[1,53]} = 166.6$, $p < 0.001$, Fig. 4*a*; hockey stick: $\log_e \alpha = 1.26 - 0.60\log_e SPR_{F=0}$, $r^2 = 0.57$, $F_{[1,35]} = 44.9$, $p < 0.001$, Fig. 4*b*). Stocks with a high $SPR_{F=0}$ also had the strongest compensation ratio (Ricker: $\log_e CR = 3.24 + 0.28\log_e SPR_{F=0}$, $r^2 = 0.23$, $F_{[1,53]} = 15.35$, $p < 0.001$, Fig. 4*c*; hockey stick: $\log_e CR = 2.25 + 0.42\log_e SPR_{F=0}$, $r^2 = 0.34$, $F_{[1,35]} = 17.68$, $p < 0.001$, Fig. 4*d*).

There are significant correlations between individual life history traits and $\tilde{\alpha}$ and CR (Table 1). Five of the twenty relationships were significant for the two recruitment models (Table 1). By chance alone, we would expect only one to be a false positive. Broadly speaking, large-bodied, late-maturing stocks had stronger density dependence at large stock sizes. However, individual life history traits had little explanatory power (Table 1). This was because individual life history traits could not predict both α and $SPR_{F=0}$, the major components of $\tilde{\alpha}$ (see eq. 10). However, they did provide an indirect estimate of $\tilde{\alpha}$ via their relationships with $SPR_{F=0}$, as well as α (Tables 2 and 3). Stocks with high α were typically

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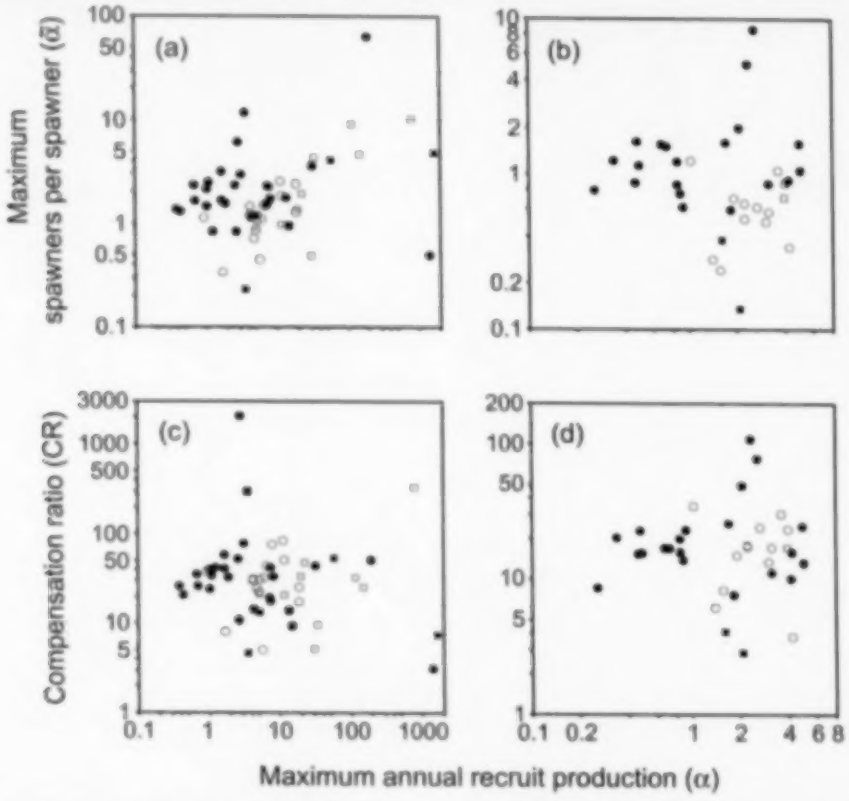
Fig. 3. Relationships between $\log_e$ maximum annual recruit production (α) and $\log_e$ maximum spawners per spawner ($\bar{\alpha}$) (*a*, *b*) and $\log_e$ compensation ratio (CR) (*c*, *d*) derived for stocks based on (*a*, *c*) Ricker and (*b*, *d*) hockey stick spawner–recruit models. □, Clupeiformes; ●, Gadiformes; ■, Perciformes; ○, Pleuronectiformes.



small-bodied, early-maturing, and had low fecundity and a fast generation time (Table 2). Life history traits explained between 8% and 67% of the variation in $SPR_{F=0}$ among stocks, with high $SPR_{F=0}$ among stocks with a heavy maximum body weight, slow growth rate, late age at maturity, high fecundity, and long generation time (Table 3).

Recall that 18 stocks did not fit the hockey stick model of recruitment. On closer inspection, 16 of these stocks had $SPR_{F=0}$ values of less than 1 kg (Figs. 4*b* and 4*d*). For stocks ≥1 kg $SPR_{F=0}$, a multiple regression based on individual life histories confirmed that the strongest CR was found in large-bodied, late-maturing stocks, with relatively low fecundity at maturity (Table 4).

Discussion

Our results have revealed that strong density-dependent recruit mortality at high spawner abundance occurs in marine fish stocks that produce high maximum numbers of spawners per spawner at low abundance. The correlation between density-related recruitment processes taking place at opposite ends of the spawner abundance spectrum is strongly mediated by life history traits. Stocks with high lifetime $SPR_{F=0}$ had low α and also longer generation times associated with multiple breeding over their lifetime. These results support other studies that link individual life history traits to rates of annual recruitment (Myers et al. 1997; Hutchings 2001; Denney et al. 2002). They also suggest that fish exhibit a life history continuum that is similar to birds, ranging from "highly reproductive species" to "survivor species" (Sæther and Bakke 2000). More importantly, our work provides the first evidence for a relationship between life history traits and density-dependent recruitment at large population sizes, whereas Sæther and Bakke (2000) did not take density dependence into account.

Stocks with high $SPR_{F=0}$ are composed of individuals that show the expected trade-off between low α and high rates of repeat spawning over a lifetime. This bet-hedging strategy is common among species with a long reproductive lifespan and an extended age structure, which have the opportunity to spread their reproductive effort over a greater number of annual production cycles (Warner and Chesson 1985; Stearns 1992). Weak density-dependent recruit mortality (compensation) among stocks with low $SPR_{F=0}$ reflects the life history strategy of small, fast-growing species that exploit unpredictable productivity. This responsiveness is thought to create population dynamics with a high variance in population numbers. Slow-growing and late-maturing species have more stable populations and constant low annual recruitment at high population sizes.

The similarity of results for Ricker and hockey stick models of recruitment suggests a general pattern of association be-

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Fig. 4. Relationship between $\log_e$ maximum spawners per recruit in the absence of fishing ($SPR_{F=0}$) and (*a*, *b*) $\log_e$ maximum annual recruit production (α) and the (*c*, *d*) $\log_e$ compensation ratio (CR) for (*a*, *c*) Ricker and (*b*, *d*) hockey stick spawner–recruit models. □, Clupeiformes; ●, Gadiformes; ■, Perciformes; ○, Pleuronectiformes.

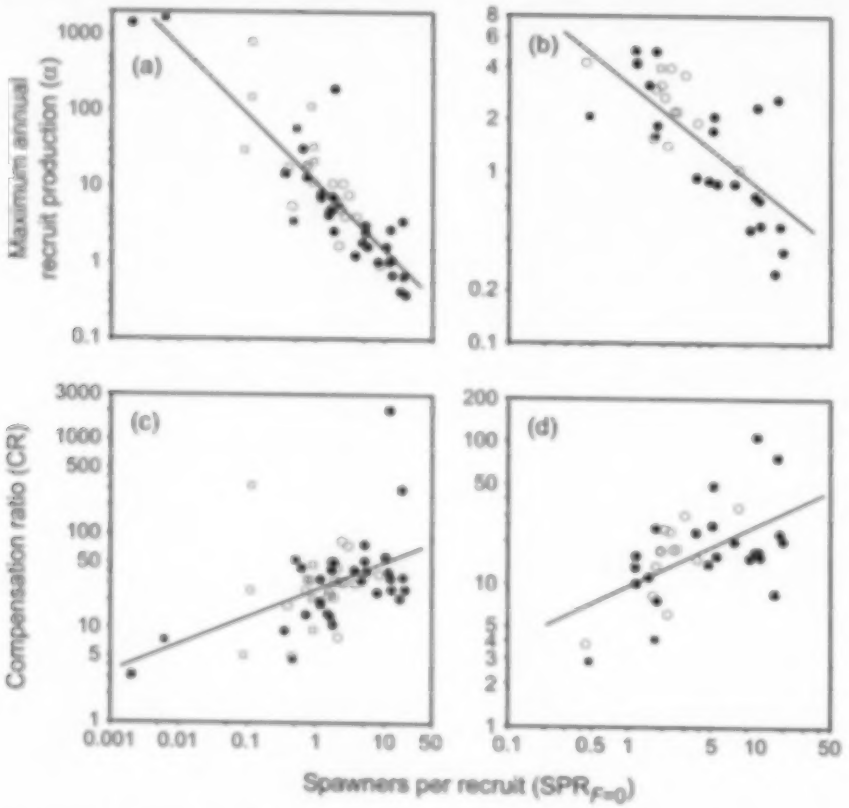

Table 1. Relationships between stock $\log_e$ life histories and (*i*) $\log_e$ maximum spawners per spawner ($\bar{\alpha}$) and (*ii*) $\log_e$ compensation ratio (CR), derived from Ricker and hockey stick spawner–recruit relationships.

	Ricker				Hockey stick			
Life history trait	Slope	Model r^2	N	P	Slope	Model r^2	N	P
$\log_e \bar{\alpha}$								
Maximum weight (W_∞)	–0.01	<0.01	45	0.873	0.33	0.49	30	<0.001
Growth rate (κ)	0.27	0.04	45	0.181	–0.10	0.01	30	0.691
Age at maturity (T_{mat})	–0.08	<0.01	53	0.729	0.46	0.07	35	0.129
Fecundity (Fec_{mat})	0.03	<0.01	43	0.721	0.28	0.20	27	0.016
Generation time (G)	–0.06	<0.01	43	0.899	0.19	<0.01	27	0.767
$\log_e$ CR								
Maximum weight (W_∞)	0.14	0.08	45	0.066	0.21	0.23	30	0.006
Growth rate (κ)	–0.09	<0.01	45	0.700	–0.07	<0.01	30	0.766
Age at maturity (T_{mat})	0.46	0.05	53	0.091	0.72	0.17	35	0.011
Fecundity (Fec_{mat})	0.24	0.16	43	0.007	0.13	0.05	27	0.256
Generation time (G)	0.97	0.09	43	0.048	0.77	0.07	27	0.189

tween $\bar{\alpha}$ at low spawner abundance and density dependence at high abundance. The assumed form of density-dependent recruitment, which is rarely clear-cut, may therefore make little difference if we want to establish whether a stock has strong recruit potential at low stock sizes or has the capacity to buffer against the early phases of exploitation at high stock sizes (high compensatory reserve). This is not to suggest that alternative spawner–recruit functions are redundant, rather that difficulties in identifying their shape or exact parameterisation need not be a fundamental barrier to an assessment of how a stock might respond to exploitation, or indeed how it recovers from it.

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Table 2. Partial correlations between stock $\log_e$ life histories and $\log_e$ maximum annual recruit production (α) derived from Ricker and hockey stick spawner–recruit relationships while controlling for age at recruitment.

	Ricker				Hockey stick			
Life history trait	Partial correlation	Model r^2	N	P	Partial correlation	Model r^2	N	P
Maximum weight (W_∞)	–0.67	0.60	45	<0.001	–0.42	0.31	30	0.021
Growth rate (κ)	0.27	0.33	45	0.069	–0.33	0.25	30	0.073
Age at maturity (T_{mat})	–0.43	0.41	53	0.001	–0.11	0.18	35	0.522
Fecundity (Fec_{mat})	–0.64	0.53	43	<0.001	–0.59	0.38	27	0.001
Generation time (G)	–0.50	0.41	43	0.001	0.16	0.08	27	0.417
Spawners per recruit ($SPR_{F=0}$)	–0.83	0.77	53	<0.001	–0.70	0.57	35	<0.001

Table 3. Linear regressions between $\log_e$ life history characteristics of stocks and the $\log_e$ spawners per recruit ($SPR_{F=0}$).

Life history trait	Constant	Slope	Model r^2	F	df	P
Maximum weight (W_∞)	0.09	0.61	0.67	88.9	144	<0.001
Growth rate (κ)	–0.5	–0.59	0.08	3.7	144	0.062
Age at maturity (T_{mat})	–1.37	2.01	0.36	29.6	152	<0.001
Fecundity (Fec_{mat})	–7.21	0.65	0.45	34.1	143	<0.001
Generation time (G)	–6.43	3.67	0.49	41.0	142	<0.001

Table 4. Results of the multiple regression between $\log_e$ life histories and $\log_e$ compensation ratio (CR) for (*i*) Ricker and (*ii*) hockey stick recruitment models.

Ricker[a]				
Trait	Coefficient	SE of coefficient	t_{22}	P
Constant	2.13	0.49	4.31	<0.001
Maximum weight (W_∞)	0.18	0.10	1.76	0.090
Age at maturity (T_{mat})	1.06	0.46	2.30	0.029
Hockey stick[b]				
Trait	Coefficient	SE of coefficient	t_{19}	P
Constant	4.69	1.61	2.92	0.009
Maximum weight (W_∞)	0.32	0.10	3.06	0.007
Age at maturity (T_{mat})	0.72	0.33	2.17	0.043
Fecundity (Fec_{mat})	–0.25	0.14	–1.80	0.088

Note: Data were limited to those stocks whose $SPR_{F=0}$ is ≥1 kg, which equates to a maximum weight of approximately 1.5 kg or heavier. SE, standard error.

[a]Multiple $r^2 = 0.29$; $F_{3,28} = 5.66$; $p = 0.009$.

[b]Multiple $r^2 = 0.50$; $F_{3,19} = 6.42$; $p = 0.003$.

Individual life history traits were poor predictors of the two standardized measures of recruitment: $\tilde{\alpha}$ and CR. The positive relationship between maximum weight and $\tilde{\alpha}$ and CR derived from the hockey stick method could be due to a bias against smaller-bodied stocks. These stocks were excluded from the regression because the hockey stick model did not fit (Appendix Table A2). Indeed, we showed that these nonfitting stocks had an average value of α (derived from the Ricker model) that was 26 times greater than those that did fit hockey stick models.

A composite measure of life history traits ($SPR_{F=0}$) summarized the important elements from several traits and was much more informative. Unfortunately, few species have the age-specific life history data and estimates of natural mortality necessary to calculate $SPR_{F=0}$. Natural mortality is particularly difficult to estimate, and stock assessments often resort to giving this parameter a default estimate, such as 0.2. However, a multiple regression using more easily measured traits such as body size and age at maturity provided a reasonable prediction of CR for both Ricker and hockey stick recruitment models. Body size alone was a strong predictor of $SPR_{F=0}$, which would also enable an indirect estimate of the CR. Life history invariants and scaling rules could also be applied where direct measures are missing (Pope et al. 2000; Dulvy et al. 2004).

Iteroparity is thought to have evolved as a bet-hedging strategy to compensate for years of recruitment failure due to adverse environmental conditions (Stearns 1976; Hutchings 2002). This environmental component to recruitment implies a density-independent process. This might appear to contradict our evidence that bet-hedgers, which are typically large, late-maturing, and long-lived, have strong density-dependent recruit mortality. The strong density dependence among these species may be explained by compe-

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tition among both recruits and adults, which depresses recruit survival at high densities. We suggest that both the negative intercohort effects on recruit survival and the strategy of producing large numbers of small offspring are not mutually exclusive. The outcome would be that bet-hedging can still exploit favourable environments and show unpredictable recruitment patterns, but individuals at high densities suffer a reduction in $\bar{\alpha}$.

The environment is also expected to affect the recruit survival of pelagic and demersal fishes in different ways. For example, pelagic fishes are thought to track and exploit environmental conditions and show very little increase in recruit mortality with stock size (weak density dependence or compensation). However, since most pelagic species are small and short-lived, we cannot say whether or not pelagic and demersal fishes have different constraints upon maximizing recruit survival than would be predicted from life histories alone. A more wide-ranging pelagic data set is required to adequately address this question.

This study can be used to predict how stocks will respond to fishing and to assess vulnerability to extinction, particularly in data-poor situations. Stocks with low $SPR_{F=0}$ have weak density dependence and high annual production; at the outset of fishing, even low fishing mortality could rapidly deplete stocks with little compensatory recruitment, but show high resilience to extinction at very low stock sizes (e.g., Atlantic herring, *Clupea harengus*). Conversely stocks with strong density dependence have a greater compensatory reserve that is initially very productive, but then collapse through low resilience at small stock sizes as a result of low annual recruit production (e.g., Atlantic cod, *Gadus morhua*). The power of basic life history traits to predict $SPR_{F=0}$ also facilitates a precautionary approach to fisheries management because $SPR_{F=0}$ is already used to derive the biological reference points that indicate recruitment overfishing (Gabriel et al. 1989; Mace and Sissenwine 1993). For conservation managers, our results offer a further biological basis for developing meaningful vulnerability criteria for fishes that include density dependence (Hutchings 2001; Reynolds et al. 2002; Dulvy et al. 2003).

Future development of this approach could include habitat and environmental variables (such as temperature and productivity) to account for the remaining variance in density dependence. A community approach could also address the potential interactions among recruits of different species competing for similar resources during early life stages. Clearly, the timing and location of reproduction and the early life history combinations of developing offspring will also affect annual recruitment; these have not been considered in this study.

In conclusion, we have shown that a simple composite measure of life history (spawners per recruit) is correlated with density-dependent recruitment in commercially exploited fish populations. The correlation with density dependence remains when $SPR_{F=0}$ are combined with annual recruitment to yield the maximum number of spawners per spawner. We also found that populations that grow slowly from small sizes have the strongest density-dependent recruitment at large population sizes. These results suggest that we can build a framework based on life histories to predict marine fish population dynamics across species and populations.

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Appendix A

Appendix appears on the following pages.

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Table A1. Summary of stock maximum weight (W_∞), growth rate (κ), age at 50% maturity (T_{mat}), fecundity at maturity (Fec_{mat}), generation time (G), and the maximum age class in the life history model (i_{max}) based on postrecruitment, age-specific values.

Stock[a]	$SPR_{F=0}$ (kg)	W_∞[b] (kg)	κ (year^{-1})	T_{mat} (years)	Fec_{mat}	G (years)	i_{max} (years)	M
European anchovy (*Engraulis encrasicolus*)								
BB	0.115	0.07	0.25	0.50	1 52 800	3.1	5	0.12
Atlantic cod (*Gadus morhua*)								
CS and West Channel	19.959	17.61	0.37	2.21	2 014 900	5.1	7	0.20
Faroe Plateau	11.577	76.13	0.07	2.97	—	—	9	0.20
Iceland	18.851	33.61[c]	0.12	5.06	520 460	10.2	14	0.20
Irish Sea	12.687	86.17	0.11	2.06	1 522 700	5.0	7	0.20
Kattegat	7.864	19.89	0.23	2.24	—	—	8	0.20
Northeast Arctic	12.078	129.20	0.07	6.95	1 361 800	10.4	13	0.20–0.38
NS, Skagerrak, and East Channel	18.107	18.99	0.24	3.73	806 250	7.7	11	0.20–0.80
West Baltic	5.264	—	—	2.82	935 830	5.5	7	0.20–0.24
West Scotland	12.972	28.53	0.20	2.02	917 720	5.1	7	0.20
Blue whiting (*Micromesistius poutassou*)								
Northern ICES	0.356	0.33[c]	0.15	2.24	19 323	6.2	10	0.20
Fourspotted megrim (*Lepidorhombus boscii*)								
Iberia	0.384	—	—	0.98	27 870	4.2	7	0.20
Greenland halibut (*Reinhardtius hippoglossoides*)								
Northeast Arctic	8.568	—	—	9.17	16 250	12.7	15	0.15
Haddock (*Melanogrammus aeglefinus*)								
Faroe Plateau	5.610	5.11	0.18	3.07	—	—	8	0.20
Iceland	4.724	6.89	0.17	3.76	—	—	9	0.20
Northeast Arctic	3.726	3.18	0.22	5.85	939 630	8.4	11	0.20–0.29
NS, Skagerrak, and Kattegat	1.827	3.24	0.17	2.52	125 740	7.1	10	0.20–2.05
Rockall	1.193	0.79	0.21	2.50	122 610	4.9	7	0.20
West Scotland	1.735	1.55	0.22	1.96	41 326	5.4	8	0.20
European hake (*Merluccius merluccius*)								
Iberia	1.501	5.50[c]	0.15	3.19	165 850	6.2	8	0.20
NS, CS, and Channel	1.778	14.21[c]	0.13	3.78	723 880	6.4	8	0.20
Atlantic herring (*Clupea harengus*)								
CS and Southwest Ireland	0.894	0.23[c]	0.31	1.00	14 359	5.6	9	0.10–1.00
East Baltic	0.088	—	—	1.83	6 988	5.0	8	0.20–0.30
Iceland	1.885	0.41[c]	0.29	3.40	25 393	10.0	15	0.10
Irish Sea	0.745	0.20[c]	0.52	1.58	32 693	5.2	8	0.10–1.00
Norway	0.922	0.43[c]	0.23	4.28	41 177	9.3	16	0.15–0.90
NS	0.834	0.26[c]	0.45	1.84	4 422	6.2	9	0.10–1.00
West Scotland	0.923	0.24[c]	0.45	1.87	42 424	5.8	9	0.10–1.00
Atlantic horse mackerel (*Trachurus trachurus*)								
Northeast Atlantic	0.469	0.29	0.18	3.56	109 130	7.3	11	0.15
Iberia	0.513	0.31	0.22	3.75	64 468	7.9	12	0.15
Atlantic mackerel (*Scomber scombrus*)								
West stock	1.683	0.65	0.26	1.90	294 940	6.7	12	0.15
Megrim (*Lepidorhombus whiffiagonis*)								
CS, West of Ireland, West Channel, and BB	0.734	8.87	0.08	2.76	—	—	10	0.20
Iberia	0.442	5.11	0.05	1.23	—	—	7	0.20
Norway pout (*Trisopterus esmarki*)								
NS and Skagerrak	0.002	—	—	1.23	15 125	2.1	4	1.60
European plaice (*Pleuronectes platessa*)								
CS	2.029	1.53	0.14	2.86	67 880	6.5	9	0.12
East Channel	3.031	8.77	0.05	2.90	73 638	7.2	10	0.10
Irish Sea	1.562	6.85	0.05	2.94	63 233	6.4	9	0.12
NS	3.817	1.42[c]	0.12	2.50	52 240	9.0	15	0.10

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Table A1 (*concluded*).

Stock[a]	$SPR_{F=0}$ (kg)	W_∞[b] (kg)	κ ($year^{-1}$)	T_{mat} (years)	Fec_{mat}	G (years)	t_{max} (years)	M
Skagerrak and Kattegat	2.432	—	—	2.50	49 915	7.4	11	0.10
West Channel	2.590	1.62[c]	0.16	2.86	65 241	6.9	10	0.12
Pollock (*Pollachius virens*)								
Faroe Plateau	10.556	—		5.03	—	—	12	0.20
Iceland	17.005	21.09	0.14	4.91	—	—	14	0.20
NS, Skaggerak, Kattegat, West Scotland, and Rockall	5.164	—	—	4.68	1 149 100	7.9	10	0.20
Sandeel (Ammodytoidei spp.)								
NS	0.006	0.03[c]	0.36	1.50	62	3.2	4	0.60–1.20
European pilchard (*Sardina pilchardus*)								
Iberia	0.110	0.08	0.53	0.96	379 610	3.3	6	0.33
Common sole (*Solea solea*)								
CS	1.907	0.80	0.21	3.06	100 300	7.1	10	0.10
East Channel	1.727	0.69	0.15	2.50	84 834	7.4	11	0.10
Irish Sea	1.641	0.60	0.16	2.40	83 306	6.5	10	0.10
NS	2.296	18.01	0.02	2.50	130 060	9.2	15	0.10
West Channel	2.131	0.74	0.18	3.06	139 190	7.7	12	0.10
Whiting (*Merlangius merlangus*)								
CS and West Channel	1.181	8.15	0.05	1.50	—	—	7	0.20
Irish Sea	0.637	0.61	0.35	1.50	—	—	6	0.20
NS and East Channel	0.725	0.32[c]	0.71	1.46	221 710	4.8	8	0.20–0.95
West Scotland	1.163	2.98	0.08	1.50	312 410	4.5	7	0.20

Note: Spawner per recruit ($SPR_{F=0}$) is a composite measure of an individual's lifetime contribution to spawning biomass (see eq. 4). The instantaneous rate of natural mortality (M) shows the range of age-specific values.

[a]BB, Bay of Biscay; Channel, English Channel; CS, Celtic Sea; NS, North Sea.

[b]Parameter b in the von Bertalanffy growth equation (eq. 1) was required to calculate W_∞. Values were mostly taken from regional or mean species estimates in FishBase (Froese and Pauly 2004).

[c]Data was taken from stock assessments.

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Table A2. Summary of parameters and model fits of Ricker and hockey stick spawner–recruit relationships for 18 species and 54 stocks.

	Ricker							Hockey stick								
Stock[a]	a	SD a	β (10^{-5})	SD β (10^{-7})[b]	$\hat{\sigma}$	LL	SS	α	SD α	S^*	SD S^*	$\hat{\sigma}$	LL	SS	N	R_{age} (years)
European anchovy (*Engraulis encrasicolus*)																
BB	786.35	±16.82	1.85	5.84	0.68	−247	6.6	—	—	—	—	—	—	—	15	1
Atlantic cod (*Gadus morhua*)																
CS and West Channel	0.38	<0.01	1.44	<	0.73	−249	20.6	0.34	<0.01	13 553	2 417	0.71	−250	20.4	31	1
Faroe Plateau	1.03	<0.01	2.18	<	0.58	−380	13.9	0.72	0.16	20 882	35 163	0.59	−380	13.7	39	2
Iceland	0.68	<0.01	0.11	<	0.32	−562	9.8	0.48	0.01	478 290	150 100	0.32	−563	11.1	44	3
Irish Sea	1.09	<0.01	5.95	<	0.56	−300	14.7	0.68	0.04	10 500	3 699	0.54	−301	16.5	34	0
Kattegat	1.03	<0.01	1.33	<	0.41	−296	15.3	0.84	0.03	28 733	4 178	0.43	−295	17.5	30	1
Northeast Arctic	2.78	<0.01	0.16	<	0.63	−694	27.1	2.35	<0.01	224 480	0	0.62	−696	25.3	53	3
NS, Skagerrak, and East Channel	3.53	<0.01	0.29	<	0.55	−499	20.7	2.61	0.03	159 350	13 514	0.53	−500	21.6	39	1
West Baltic	3.11	<0.01	1.32	<	0.65	−343	15.2	2.08	1.29	40 704	12 065	0.68	−342	15.4	31	1
West Scotland	0.70	0.13	2.79	14.98	0.50	−330	17.3	0.49	0.02	18 858	9 297	0.49	−330	18.3	36	1
Blue whiting (*Micromesistius poutassou*)																
Northern ICES	14.81	<0.01	0.04	<	0.67	−346	8.8	—	—	—	—	—	—	—	21	0
Fourspotted megrim (*Lepidorhombus boscii*)																
Iberia	18.35	<0.01	23.95	<	0.36	−162	1.7	—	—	—	—	—	—	—	15	1
Greenland halibut (*Reinhardtius hippoglossoides*)																
Northeast Arctic	0.94	<0.01	1.33	<	0.30	−353	5.0	1.03	0.07	20 418	19 269	0.33	−350	3.9	33	5
Haddock (*Melanogrammus aeglefinus*)																
Faroe Plateau	1.63	<0.01	2.78	<	1.01	−365	41.3	0.84	0.15	20 954	11 521	1.05	−364	40.0	39	2
Iceland	1.83	0.02	1.26	1.80	0.72	−205	9.5	0.88	<0.01	59 698	0	0.71	−205	9.4	19	2
Northeast Arctic	1.24	<0.01	0.28	<	1.24	−531	81.3	0.91	0.26	169 330	73 244	1.25	−531	81.8	49	3
NS, Skagerrak, and Kattegat	191.72	<0.01	0.23	<	1.16	−655	52.1	—	—	—	—	—	—	—	40	0
Rockall	8.07	<0.01	13.85	<	0.80	−161	11.3	4.25	0.16	3 670	132	0.80	−161	9.9	17	1
West Scotland	7.35	<0.01	2.71	<	0.86	−268	16.5	4.99	0.22	17 851	687	0.83	−268	15.8	24	1
European hake (*Merluccius merluccius*)																
Iberia	4.27	0.03	1.42	0.95	0.22	−233	2.9	3.17	0.21	34 453	5 133	0.24	−231	3.2	19	0
NS, CS, and Channel	2.60	<0.01	0.3	<	0.24	−322	2.1	1.84	0.02	152 370	7 112	0.25	−321	2.2	24	0
Atlantic herring (*Clupea harengus*)																
CS and Southwest Ireland	11.40	<0.01	0.8	<	0.54	−552	15.7	—	—	—	—	—	—	—	42	1
East Baltic	30.36	<0.01	0.05	<	0.31	−471	4.6	—	—	—	—	—	—	—	27	1
Iceland	5.10	0.24	0.27	10.37	0.48	−275	4.5	3.98	0.31	165 590	10 860	0.48	−275	4.3	20	2
Irish Sea	19.47	<0.01	2.32	<	0.49	−360	8.7								29	1
Norway	33.22	<0.01	0.01	<	1.26	−1588	327.1	—	—	—	—	—	—	—	93	0
NS	113.98	0.61	0.08	4.06	0.54	−734	40.1	—	—	—	—	—	—	—	42	0
West Scoland	21.80	0.13	0.91	0.32	0.70	−340	11.3	—	—	—	—		—	—	25	1
Atlantic horse mackerel (*Trachurus trachurus*)																
Northeast Atlantic	3.50	<0.01	0.04	<	1.01	−273	18.7	2.07	0.06	1 585 300	29 876	1.02	−273	19.1	19	0
Iberia	57.63	0.43	1.15	75.72	0.34	−249	2.3	—	—	—	—	—	—	—	17	0

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Table A2 (*concluded*).

	Ricker							Hockey stick								
Stock[a]	α	SD α	β (10^{-5})	SD β (10^{-7})[b]	$\hat{\sigma}$	LL	SS	α	SD α	S^*	SD S^*	$\hat{\sigma}$	LL	SS	*N*	R_{age} (years)
Atlantic mackerel (*Scomber scombrus*)																
Western stock	5.11	<0.01	0.04	<	0.43	−469	5.5	1.60	<0.01	2 508 200	0	0.43	−469	5.4	30	0
Megrim (*Lepidorhombus whiffiagonis*)																
CS, West of Ireland, West Channel, and BB	18.08	0.32	2.3	413.73	0.23	−230	1.0	—	—	—	—	—	—	—	17	1
Iberia	5.58	<0.01	18.14	<	0.50	−136	4.3	4.26	0.03	2 094	413	0.50	−136	4.5	15	1
Norway pout (*Trisopterus esmarkii*)																
NS and Skagerrak	1424.3	<0.01	0.43	<	0.58	−523	9.5	—	—	—	—	—	—	—	28	0
European plaice (*Pleuronectes platessa*)																
CS	6.46	0.13	47.34	149.70	0.52	−201	5.7	2.68	1.23	1 983	537	0.51	−199	5.9	23	1
East Channel	7.83	<0.01	11.66	<	0.36	−236	2.9	3.66	0.25	6 558	3 189	0.36	−236	2.9	22	1
Irish Sea	4.89	<0.01	12.28	<	0.36	−375	5.0	—	—	—	—	—	—	—	37	1
NS	4.06	<0.01	0.35	<	0.40	−605	7.2	1.92	0.25	219 400	23 202	0.41	−603	7.3	45	1
Skagerrak and Kattegat	11.04	<0.01	5.75	<	0.37	−263	5.0	2.23	0.07	22 596	685	0.45	−258	4.3	23	2
West Channel	4.13	0.09	29.97	133.97	0.50	−227	7.0	2.23	0.08	2 528	179	0.50	−226	7.6	26	1
Pollock (*Pollachius virens*)																
Faroe Plateau	1.65	<0.01	1.85	<	0.46	−399	10.5	0.46	0.03	55 047	5 371	0.51	−396	9.3	38	3
Iceland	0.43	<0.01	0.44	<	0.57	−391	12.3	0.26	0.03	132 810	134 990	0.56	−391	12.1	37	3
NS, Skaggerak, Kattegat, West Scotland, and Rockall	2.51	<0.01	0.32	<	0.43	−411	6.3	1.71	0.17	157 200	15 900	0.43	−411	6.2	32	1
Sandeel (Ammodytoidei spp.)																
NS	1643.3	33.84	0.09	0.28	0.57	−367	6.1	—	—	—	—	—	—	—	18	0
European pilchard (*Sardina pilchardus*)																
Iberia	149.06	<0.01	0.43	<	0.46	−395	6.7	—	—	—	—	—	—	—	24	0
Common sole (*Solea solea*)																
CS	6.03	<0.01	43.26	<	0.30	−287	2.8	3.15	0.14	1 486	63	0.30	−287	2.6	31	1
East Channel	11.15	<0.01	14.76	<	0.38	−214	2.9	3.02	0.17	8 289	1 561	0.39	−214	2.8	20	1
Irish Sea	4.65	<0.01	25.79	<	0.58	−276	10.6	1.56	0.16	4 305	356	0.59	−275	10.6	31	2
NS	5.11	<0.01	1.68	<	0.78	−510	26.8	4.02	<0.01	24 712	0	0.77	−511	26.1	45	1
West Channel	1.68	0.02	7.28	39.82	0.27	−306	4.7	1.41	0.03	3 673	473	0.27	−305	4.8	33	1
Whiting (*Merlangius merlangus*)																
CS and West Channel	7.31	<0.01	2.83	<	0.54	−242	6.5	4.20	<0.01	20 100	0	0.55	−242	6.2	21	0
Irish Sea	31.47	<0.01	9.83	<	0.43	−263	5.0	—	—	—	—	—	—	—	22	0
NS and East Channel	13.47	0.34	0.23	1.25	0.32	−334	2.8	—	—	—	—	—	—	—	22	1
West Scotland	7.14	<0.01	2.79	<	0.40	−283	5.3	5.02	0.12	17 425	852	0.41	−282	5.5	24	1

Note: α, maximum annual recruitment per spawner; SD, standard deviation; β governs the population size at which density dependence occurs; $\hat{\sigma}$, log error; LL, log-likelihood; SS, sum of squares; S^*, spawning stock biomass at median recruitment; *N*, length of time series; R_{age}, age-at-recruitment; —, spawner–recruit data did not fit the hockey stick relationship. Standard deviations are based on bootstrap analysis with 1000 iterations; each iteration included a full spawner–recruit fitting procedure (see Methods for details about fitting methods).

[a]BB, Bay of Biscay; Channel, English Channel; CS, Celtic Sea; NS, North Sea.

[b]A less than symbol (<) indicates SD β < 0.00000001.

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Table A3. Summary of Ricker and hockey stick estimates of maximum spawners per spawner ($\bar{\alpha}$), mean unexploited spawning stock biomass ($SSB_{F=0}$), and the compensation ratio (CR).

	Ricker			Hockey stick		
Stock[a]	$\bar{\alpha}$	$SSB_{F=0}$	CR	$\bar{\alpha}$	$SSB_{F=0}$	CR
European anchovy (*Engraulis encrasicolus*)						
BB	10.24	314 370	330.97	—	—	—
Atlantic cod (*Gadus morhua*)						
CS and West Channel	1.38	226 180	25.81	1.22	282 820	20.47
Faroe Plateau	2.16	169 190	40.07	1.51	562 700	16.98
Iceland	2.32	3 307 300	34.83	1.63	11 397 000	22.94
Irish Sea	2.52	59 493	34.45	1.56	201 600	17.02
Kattegat	1.47	238 660	24.12	1.20	547 050	19.99
Northeast Arctic	6.09	4 699 100	2081.28	5.14	24 524 000	109.25
NS, Skagerrak, and East Channel	11.59	1 945 900	297.86	8.57	12 642 000	78.78
West Baltic	2.96	333 570	77.69	1.99	1 672 700	49.72
West Scotland	1.64	116 380	25.81	1.14	323 900	15.61
Blue whiting (*Micromesistius poutassou*)						
Northern ICES	0.96	6 308 000	9.46	—	—	—
Fourspotted megrim (*Lepidorhombus boscii*)						
Iberia	1.28	12 000	17.65	—	—	—
Greenland halibut (*Reinhardtius hippoglossoides*)						
Northeast Arctic	1.12	273 160	37.91	1.22	796 560	34.8
Haddock (*Melanogrammus aeglefinus*)						
Faroe Plateau	1.65	133 160	40.45	0.86	387 290	15.9
Iceland	1.57	274 450	32.17	0.76	832 930	13.95
Northeast Arctic	0.84	1 320 300	42.03	0.62	3 705 000	23.34
NS, Skagerrak, and Kattegat	63.5	1 717 700	50.63	—	—	—
Rockall	1.75	25 326	33.4	0.92	57 947	15.77
West Scotland	2.31	138 050	41.91	1.57	435 790	24.7
European hake (*Merluccius merluccius*)						
Iberia	1.16	186 260	14.17	0.86	361 320	11.26
NS, CS, and Channel	0.84	801 420	10.96	0.59	1 179 900	7.71
Atlantic herring (*Clupea harengus*)						
Celtic Sea and Southwest Ireland	0.97	378 280	20.9	—	—	—
East Baltic	0.49	3 407 500	5.2	—	—	—
Iceland	0.91	1 147 400	21.36	0.71	2 737 600	17.22
Irish Sea	1.38	150 900	32.94	—	—	—
Norway	4.27	19 432 000	9.52	—	—	—
NS	9.04	4 251 400	32.8	—	—	—
West Scotland	1.92	425 440	47.24	—	—	—
Atlantic horse mackerel (*Trachurus trachurus*)						
Northeast Atlantic	0.23	3 711 400	4.66	0.14	4 534 800	2.86
Iberia	4.12	346 540	54	—	—	—
Atlantic mackerel (*Scomber scombrus*)						
Western stock	1.20	5 851 600	13.27	0.38	10 410 000	4.15
Megrim (*Lepidorhombus whiffiagonis*)						
CS, West of Ireland, West Channel, and BB	2.40	139 870	25.07	—	—	—
Iberia	0.45	9 374	4.99	0.34	8 749	3.82
Norway pout (*Trisopterus esmarki*)						
NS and Skagerrak	0.50	264 810	3.11	—	—	—

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Table A3 (*concluded*).

Stock[a]	Ricker			Hockey stick		
	$\bar{a}$	$SSB_{F=0}$	CR	$\bar{a}$	$SSB_{F=0}$	CR
European plaice (*Pleuronectes platessa*)						
CS	1.48	7 973	43.41	0.61	34 707	24.25
East Channel	2.26	37 186	76.39	1.05	231 540	30.5
Irish Sea	0.86	25 398	22.64	—	—	—
NS	1.47	983 620	30.46	0.70	3 148 900	15.18
Skagerrak and Kattegat	2.56	76 890	83.39	0.52	390 830	17.52
West Channel	1.21	11 466	30.87	0.65	42 400	17.81
Pollock (*Pollachius virens*)						
Faroe Plateau	3.15	219 630	57.56	0.88	844 890	15.35
Iceland	1.31	687 530	20.61	0.79	1 612 500	8.69
NS, Skaggerak, Kattegat, West Scotland, and Rockall	2.35	1 243 000	52.03	1.60	3 825 800	25.9
Sandeel (*Ammodytoidei* spp.)						
NS	4.82	2 229 000	7.43	—	—	—
European pilchard (*Sardina pilchardus*)						
Iberia	4.62	754 390	25.07	—	—	—
Common sole (*Solea solea*)						
CS	1.1	8 031	32.27	0.57	25 046	17.17
East Channel	1.83	26 551	50.29	0.50	113 890	13.36
Irish Sea	0.73	12 458	24.86	0.24	35 165	8.36
NS	1.12	204 050	30.99	0.88	580 530	23.49
West Channel	0.34	28 768	8.06	0.29	24 954	6.18
Whiting (*Merlangius merlangus*)						
CS and West Channel	1.57	101 720	17.81	0.90	203 150	10.11
Irish Sea	3.64	38 553	44.29	—	—	—
NS and East Channel	1.77	1 158 300	14.07	—	—	—
West Scotland	1.50	105 760	19.13	1.06	233 930	13.31

[a]BB, Bay of Biscay; Channel, English Channel; CS, Celtic Sea; NS, North Sea.

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Improving the definition of fishing effort for important European fleets by accounting for the skipper effect

Paul Marchal, Bo Andersen, David Bromley, Ane Iriondo, Stéphanie Mahévas, Floor Quirijns, Brian Rackham, Marina Santurtún, Nicola Tien, and Clara Ulrich

Abstract: The scope of this paper is to quantify, for a wide selection of European fisheries, fishing tactics and strategies and to evaluate the benefits of adjusting the definition of fishing effort using these elements. Fishing tactics and strategies were identified by métiers choices and a series of indices. These indices have been derived to reflect shifts in tactics (within a fishing trip) and in strategies (within a year). The Shannon–Wiener spatial diversity indices of fishing tactics (FT_SW) and strategies (YE_SW) had the greatest impact on catch rates. In particular, FT_SW was always negatively correlated to catch rates. One may anticipate that during a fishing trip, vessels with high FT_SW have been searching fish aggregations for a long time, while vessels with low FT_SW have been more efficient in finding these aggregations. The linkage between YE_SW and catch rates was of a more complex nature. Adjusting fishing effort by means of (*i*) the métier effect and (*ii*) the indices of tactics and strategies generally led to a substantial gain in the precision of the relationship between fishing mortality and fishing effort.

Résumé : L'objectif de cette étude est de quantifier, pour une large sélection de pêcheries européennes, les tactiques et stratégies de pêche, et d'évaluer dans quelle mesure ces éléments peuvent être utilisés pour mieux ajuster l'effort de pêche. Les tactiques et stratégies de pêche ont été identifiées par les choix de métiers et une série d'indices. Ces indices ont été calculés pour quantifier les changements de tactique (au cours d'une marée) et de stratégie (au cours d'une année). Les indices de Shannon–Wiener décrivant la distribution spatiale de l'effort de pêche au cours d'une marée (FT_SW) et d'une année (YE_SW) ont eu l'effet le plus important sur les taux de capture. En particulier, FT_SW était négativement corrélé aux taux de capture pour tous les cas d'étude. Ce résultat était prévisible. Au cours d'une marée, les bateaux caractérisés par un FT_SW élevé ont vraisemblablement cherché les agrégations de poisson pendant une longue période, tandis que les bateaux caractérisés par un faible FT_SW auront été plus efficaces pour localiser ces agrégations. Le lien entre YE_SW et les taux de capture était d'une nature plus complexe. L'ajustement de l'effort au moyen, (*i*) de l'effet métier et, (*ii*) des indices de tactique et de stratégie, conduit généralement à un gain substantiel de précision de la relation entre effort de pêche et mortalité par la pêche.

Introduction

A common concern of fisheries managers is to be able to reconcile the objectives of maintaining fisheries profit while safeguarding the fish resources, especially when these are exploited beyond biologically safe limits. In European Union (EU) waters, the management of fisheries and fish resources has been adversely altered by (*i*) the lack of consensus on management targets and strategies and also (*ii*) the poor understanding of the links among management tools, fleet developments, and the pressure exerted on fishing communities. A major ongoing issue, relevant to both points (*i*) and (*ii*), is the exploration of the relationship between fishing mortality (F) and fishing effort (E). A common as-

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sumption underlying fish stock assessments and fisheries management is that F is directly proportional to E: $F(t) = qE$, where q is the catchability coefficient. However, it has been ascertained in a number of fisheries studies that the relationship between F and E could be of a more complex nature, as a result of combined mechanisms including changes in fish accessibility (Swain et al. 1994), technical creeping (Mahévas et al. 2004), and shifts in fishing regimes (Pascoe et al. 2001).

Defining effort such that fluctuations in E can be related to fluctuations in F would positively impact the reliability of catch rates as stock abundance indicators, the precision of stock assessments tuned by these catch rates, and eventually the scientific basis for managers decision-making (Cook and Armstrong 1985; Arreguin-Sanchez 1996; Marchal et al. 2003). In addition, defining effort such that the correlation between F and E increases would allow fisheries managers to evaluate the impact of effort-based management regimes on the pressure really exerted on fish stocks (Overholtz et al. 1995; Ulrich et al. 2002). The reliability of the relationship between F and E depends on the precision of both the measurement of E and the estimate of F. This paper examines the issue of better measuring E.

E is traditionally estimated by combining available measurements of fishing capacity (fixed production inputs) and fishing activity (variable production inputs). Fishing capacity is frequently approached by some attribute of the operating vessel (vessel length, engine power, gross tonnage) (Gulland 1964; Robson 1966; Marchal et al. 2002), but a number of investigations have been carried out to incorporate other elements, including gear technology and equipment on board, in the definition of E (Hovgaard 1996; Rose and Nunnallee 1998; Sangster and Breen 1998). Fishing activity is typically estimated by the time spent fishing during a fishing trip. Such a definition, however, does not account for the skipper effect, which can be defined as the ability of a skipper to locate high fish densities and to harvest them. Some approaches have been developed to incorporate fishing tactics and strategies in the definition of E (Hilborn 1985; Abrahams and Healey 1990; Rijnsdorp et al. 1998).

The scope of this paper is to quantify, for a wide selection of European fleets, fisheries and stocks, fishing tactics and strategies (skipper effect), and to evaluate the benefits of adjusting E using the skipper effect. First, a comprehensive suite of indices of fishing tactics and strategies is calculated for each vessel of the fleets under investigation. These indices reflect different characteristics of the fishermen's fishing behaviour, which may be traditional (vs. exploratory), stationary (vs. mobile), or random (vs. aggregative). The correlations between these indices will be examined. Second, the vessels' catch rates are modelled using generalized linear models (GLMs), with métiers (hereby defined as a set of vessel voyages targeting the same species in the same area and with similar gears) and the indices of fishing tactics or strategies as explanatory variables. This method is applied to identify the indices that best contribute to the variations of catch rates. In addition, nominal E is translated into effective E using the most important elements of fishing tactics or strategies identified above. Third, the benefits of modelling catch rates and of adjusting E are evaluated by contrasting E with available estimates of F.

The methods developed in the different parts of the study are applied to EU fleets of different nationalities (Denmark, France, the Netherlands, the Basque Country (Spain), England (UK)) harvesting different species (anglerfish (*Lophius* spp.), gadoids, European hake (*Merluccius merluccius*), flatfish, other deepwater species) in different fishing areas (Bay of Biscay, Celtic Sea, Western Scotland, North Sea).

Materials and methods

Data

The different fishing areas, as encoded by the ICES (International Council for the Exploration of the Sea), are shown (Fig. 1). The catch and effort data used for this analysis have been derived from national fisheries databases. Data are disaggregated by vessel, fishing trip, statistical rectangle (surface: 1° longitude × 0.5° latitude or approximately 30 nautical miles (n.mi.) × 30 n.mi. (1 n.mi. = 1.853 km)), and gear used. The recorded vessels characteristics are length, tonnage, and horsepower. The type of gear (otter trawl, pair trawls, beam trawl, gill net, etc.) and, for most fleets, the mesh size used, were also made available.

Units for E differed across countries: days fishing (Danish, Dutch, and English fleets), hours fishing (Basque and French fleets). The way E was allocated among statistical rectangles during the same fishing trip also differed among countries. The proportion of E allocated in each rectangle was directly available from logbooks for the French and Basque fleets, but not for the other fleets, where it had to be estimated. In the Danish and English databases, the same proportion of E was allocated to all the rectangles visited during the same fishing trip. In the Dutch database, the spatial allocation of E was calculated in proportion to the landings value achieved in each rectangle. To reduce the effect of outliers, only the fishing trips where the landings of the species being analyzed were higher than 5 kg were selected.

Vessels were grouped into fishing fleets, while fishing trips were grouped into métiers. Fleets and métiers have here been defined consistent with recommendations from ICES (2003*a*). A fleet was defined as a group of vessels sharing similar characteristics in terms of technical features and (or) major activity. Métier has already been defined. Fleet and métier definitions were made available by each participating country prior to the current investigation. The methods used to define these fleets and métiers differed from one country to another. For example, some countries included landing harbor to characterize fleets, and others did not. Some countries used catch profiles to identify métiers (e.g., Danish "cod" gill-netters fishing in the North Sea), while others used a combination of inputs (e.g., Dutch beam trawlers fishing in the North Sea with a mesh size included in the range 80–99 mm). In total, 17 fleets and 54 métiers were identified and investigated. The characteristics of the different fleets and métiers considered in this paper are summarized (Tables 1 and 2).

Total international landings and estimated fishing mortality by stock were derived from ICES advice (ICES 2003*b*). Separate F estimates were given for the two anglerfish species (*Lophius budegassa* and *Lophius piscatorius*). An overall anglerfish F was calculated by averaging the landings-weighted F of each of these two species. No F estimates

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Fig. 1. Map of the fishing areas of the International Council for the Exploration of the Sea (ICES).

were available for roundnose grenadier (*Coryphaenoides rupestris*), black scabbardfish (*Aphanopus carbo*), and blue ling (*Molva dypterygia*). The information for the most important stocks harvested by the fleets being investigated is summarized for 2002 (Table 3).

Fishing tactics and strategies

Definitions

We define here fishing tactics as the sequence of decisions taken at sea by a skipper at the scale of the fishing trip; fishing strategies are the sequence of decisions taken at sea by a skipper at the scale of a year (that is the sum of the fishing tactics over the year). The sequence of decisions may include spatial effort allocation, gear, mesh size, and (or) métier choice. These definitions are consistent with those proposed by Laloë and Samba (1991) and Laurec et al. (1991).

Fishing tactics may be characterized through two types of variables: the métier chosen by the skipper during one fishing trip and indices that characterize the general behavior of the skipper at the scale of the fishing trip (traditional vs. exploratory, stationary vs. mobile, or random vs. aggregative). Fishing strategies may be characterized through indices that quantify the general behavior of the skipper at the scale of the year (traditional vs. exploratory, stationary vs. mobile, or random vs. aggregative). The skipper's general behavior is

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Table 1. Summary of the international fleets investigated.

Country	Period	Harbour(s)	Main gear	Boat length (m) or power (hp)	Reference name
Denmark	1999–2003	West Jutland	GN	0–12 m	FL01
				12–15 m	FL02
				15–18 m	FL03
				18–24 m	FL04
			DSN	15–18 m	FL05
				18–24 m	FL06
			OTB	15–18 m	FL07
				18–24 m	FL08
UK (England)	2000–2002	East coast	OTB	10–19 m	FL09
			TBB	30–39 m	FL10
France	1999–2003	Boulogne	OTB	40+ m	FL11
		South Brittany	OTB	24+ m	FL12
Netherlands	1995–2002	All	TBB	300–1500 hp	FL13
				1500+ hp	FL14
Spain (Basque Country)	1995–2003	Ondorroa	OTB	20–29	FL15
				30–39	FL16
		Pasaia	OTB	30–39	FL17

Note: DSN, Danish seiners; GN, gill-netters; OTB, otter trawlers; TBB, beam trawlers.

characterized by (*i*) métier choices and (*ii*) indices of fishing tactics and strategies, which are described below. In most cases (unless stated explicitly), these indices may be calculated for each vessel, by fishing trip (index of fishing tactics), and by year (index of fishing strategies).

Trip- and annual-based indices of spatial diversity

These indices describe how stationary or how mobile skippers have been with regards to the number of fishing grounds visited during a fishing trip or a year. Abrahams and Healey (1990) used the Shannon–Wiener diversity index, which is derived from information theory. For each vessel v deploying nominal fishing effort En in each ICES rectangle $a \in A$ during fishing trip i, the index of fishing tactics FT_SW may be calculated as

$$(1) \qquad \mathrm{FT\_SW}_{v,i} = -\sum_{a \in A}\left(\frac{\mathrm{En}_{v,i,a}}{\mathrm{En}_{v,i,A}}\right)\ln\left(\frac{\mathrm{En}_{v,i,a}}{\mathrm{En}_{v,i,A}}\right)$$

For each vessel v deploying nominal fishing effort En in each ICES rectangle $a \in A$ during year y, the index of fishing strategy YE_SW may be calculated as

$$(2) \qquad \mathrm{YE\_SW}_{v,y} = -\sum_{a \in A}\left(\frac{\mathrm{En}_{v,y,a}}{\mathrm{En}_{v,y,A}}\right)\ln\left(\frac{\mathrm{En}_{v,y,a}}{\mathrm{En}_{v,y,A}}\right)$$

The minimal value FT_SW = 0 occurs if only one fishing area is visited by a vessel during the same fishing trip; similarly, YE_SW = 0 if during the same year. The indices increase as vessels distribute E equally among a large number of fishing areas. If E is distributed evenly across rectangles within a trip (respective values within a year are shown in parentheses), then

$$\mathrm{FT\_SW} = \ln(A) \qquad (\mathrm{YE\_SW} = \ln(A))$$

If E is distributed unevenly across rectangles within a trip, then

$$\ln(A-1) < \mathrm{FT\_SW} < \ln(A)$$

$$(\ln(A-1) < \mathrm{YE\_SW} < \ln(A))$$

Annual index of métier diversity

This index describes how stationary or how mobile skippers have been with regards to the number of métiers selected during a year. This index, which has been used by Ulrich and Andersen (2004), may be defined similarly to the Shannon–Wiener index of spatial diversity (eq. 2). For each vessel v deploying nominal fishing effort En within each métier $m \in M$ during year y, the index of fishing strategy YE_SW_METIER may be calculated as

$$(3) \qquad \mathrm{YE\_SW\_METIER}_{v,y} = -\sum_{m=1}^{M}\left(\frac{\mathrm{En}_{v,y,m}}{\mathrm{En}_{v,y,M}}\right)\ln\left(\frac{\mathrm{En}_{v,y,m}}{\mathrm{En}_{v,y,M}}\right)$$

The minimal value YE_SW_METIER = 0 occurs if only one métier is carried out by a vessel during the same year. The index increases as vessels distribute E equally among a large number of métiers. Note that the equivalent index of fishing tactics (FT_SW_METIER) is not calculated, as only one métier is associated to each fishing trip. If E is distributed evenly across métiers within a year, then

$$\mathrm{YE\_SW\_METIER} = \ln(M)$$

If E is distributed unevenly across métiers within a year, then

$$\ln(M-1) < \mathrm{YE\_SW} < \ln(M)$$

Trip- and annual-based indices of spatial extent

These indices describe how stationary or how mobile skippers have been with regards to the distance covered dur-

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Table 2. Summary of the main métiers investigated.

Gear[a]	Mesh size (mm) or target species[b]	ICES[c] division	Fishing ground	Reference name[d]	Target species[b]
GN	Atlantic cod	IVa–c	North Sea	DK_MET01	Atlantic cod
	European hake			DK_MET02	European plaice
	European plaice			DK_MET03	Common sole
	Common sole			DK_MET04	
	Turbot			DK_MET05	
LL	—			DK_MET06	
DSN	—	IIIaN	Skagerrak	DK_MET07	
		IId	Western Baltic	DK_MET08	
		IVa–c	North Sea	DK_MET09	
MTB	0–29	IVa–c	North Sea	DK_MET10	
OTB	70–89	IVa–c	North Sea	DK_MET11	
	90–104	IIIaN	Skagerrak	DK_MET12	
	90–104	IIIaS	Kattegat	DK_MET13	
	90+	IId	Western Baltic	DK_MET14	
	90–104	IVa–c	North Sea	DK_MET15	
	105+	IIIaN	Skagerrak	DK_MET16	
	105+	IIIaS	Kattegat	DK_MET17	
	105+	IVa–c	North Sea	DK_MET18	
OTB	0–79; mix	IVa–c	North Sea	EN_MET01	Atlantic cod
	70–99; Norway lobster	IVa–c	North Sea	EN_MET02	Haddock
	80+; haddock			EN_MET03	European plaice
	80+; mix			EN_MET04	Common sole
	80+; common sole			EN_MET05	
	100+; Atlantic cod			EN_MET06	
TBB	Mix			EN_MET07	
	80+; European plaice			EN_MET08	
	80+; common sole			EN_MET09	
OTB	80–99	VIa	Western Scotland	FR_MET01	Black scabbardfish
	80–99	VIIb–c,e–k	Celtic Sea	FR_MET02	Blue ling
	80–99	VIIIa–b	Bay of Biscay	FR_MET03	Atlantic cod
	100–109	IVa–c	North Sea	FR_MET04	Anglerfish
	100–109	VIa	Western Scotland	FR_MET05	Whiting
	100–109	VIIb–c,e–k	Celtic Sea	FR_MET06	Saithe
	100–109	VIIIa–b	Bay of Biscay	FR_MET07	
	110–129	IVa–c	North Sea	FR_MET08	
	110–129	VIa	Western Scotland	FR_MET09	
	110–129	VIIb–c,e–k	Celtic Sea	FR_MET10	
	110–129	VIIIa–b	Bay of Biscay	FR_MET11	
	130+	IVa–c	North Sea	FR_MET12	
	130+	VIa	Western Scotland	FR_MET13	
	130+	VIIb–c,e–k	Celtic Sea	FR_MET14	
TBB	0–69	IVa–c	North Sea	NL_MET01	European plaice
	70–79			NL_MET02	Common sole
	80–99			NL_MET03	
	100–119			NL_MET04	
	120–134			NL_MET05	
	135+			NL_MET06	
OTB	Mix (Baka)	VIa	Western Scotland	BC_MET01	European hake
		VIIb–c,e–k	Celtic Sea	BC_MET02	Megrim
		VIIIa–b,d	Bay of Biscay	BC_MET03	Anglerfish
	European hake	VIIb–c,e–k	Celtic Sea	BC_MET04	
		VIIIa–b,d	Bay of Biscay	BC_MET05	
PTB	VHVO[e]	VIIb–c,e–k	Celtic Sea	BC_MET06	
		VIIIa–b,d	Bay of Biscay	BC_MET07	

[a]DSN, Danish seiners; GN, gill netters; LL, long-liners; OTB, otter trawlers; MTB, multiple bottom trawlers; PTB, pair trawlers; TBB, beam trawlers.
[b]Anglerfish (*Lophius* spp.), black scabbardfish (*Aphanopus carbo*), blue ling (*Molva dypterygia*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), European hake (*Merluccius merluccius*), megrim (*Lepidorhombus* spp.), Norway lobster (*Nephrops norvegicus*), European plaice (*Pleuronectes platessa*), roundnose grenadier (*Coryphaenoides rupestris*), saithe (pollock; *Pollachius virens*), common sole (*Solea solea*), turbot (*Scophthalmus maximus*), whiting (*Merlangius merlangus*).
[c]International Council for the Exploration of the Sea.
[d]DK, Denmark; EN, England; FR, France; NL, the Netherlands; BC, Basque Country.
[e]Very high vertical opening.

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Table 3. Total international landings and mean fishing mortality (F; averaged over age classes) in 2002 for the most important stocks harvested by the fleets under investigation.

Species[a]	Stock	Landings (t)	Mean F
Atlantic cod	Celtic Sea	9 119	0.96
	North Sea	54 400	0.61
Haddock	North Sea	105 194	0.36
European hake	Northern	40 312	0.24
Megrim	Celtic Sea and Bay of Biscay	17 402	0.39
Anglerfish	Celtic Sea and Bay of Biscay	6 513	0.31
	North Sea and West Scotland	13 110	0.72
European plaice	North Sea	70 200	0.51
Common sole	North Sea	16 945	0.48
Saithe	North Sea and West Scotland	121 833	0.21
Whiting	Celtic Sea	13 083	0.53

[a]Anglerfish (*Lophius* spp.), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), European hake (*Merluccius merluccius*), megrim (*Lepidorhombus* spp.), European plaice (*Pleuronectes platessa*), saithe (pollock; *Pollachius virens*), common sole (*Solea solea*), whiting (*Merlangius merlangus*).

ing a fishing trip or a year. These indices, based on and adapted from Salthaug and Aanes (2003), are calculated for each vessel as the efforts-weighted average of all distances between fishing areas visited within one fishing trip (tactics index FT_DIST) or one year (strategy index YE_DIST):

$$\text{(4)}\qquad \text{FT\_DIST}_{v,i} = \sum_{a,a'} \left[\frac{\text{En}_{v,i,a}\,\text{En}_{v,i,a'}}{\sum_{a,a'}(\text{En}_{v,i,a}\,\text{En}_{v,i,a'})} \right] d_{v,i,a,a'}$$

$$\text{(5)}\qquad \text{YE\_DIST}_{v,y} = \sum_{a,a'} \left[\frac{\text{En}_{v,y,a}\,\text{En}_{v,y,a'}}{\sum_{a,a'}(\text{En}_{v,y,a}\,\text{En}_{v,y,a'})} \right] d_{v,y,a,a'}$$

where $d_{v,i,a,a'}$ is the Euclidian distance between fishing areas a and a', for vessel v and fishing trip i; $d_{v,y,a,a'}$ is the Euclidian distance for year y. Low values of FT_DIST indicate that vessels have a low degree of spatial extent during one fishing trip; low values of YE_DIST indicate a low degree of spatial extent during one year.

If, during a fishing trip (or year, respectively), E is evenly distributed across rectangles, we then have

$$\text{FT\_DIST}_{v,i} = \frac{2}{A(A-2)} \sum_{a,a'} d_{v,i,a,a'}$$

$$\text{YE\_DIST}_{v,y} = \frac{2}{A(A-2)} \sum_{a,a'} d_{v,y,a,a'}$$

Trip- and annual-based indices of spatial patchiness

These indices describe the patchiness of the spatial distribution of E during a fishing trip or year. Common indices of spatial patchiness that have been used in the fisheries literature are the simple coefficient of dispersion (Rijnsdorp et al. 1998) and the Clark–Evans index (Clark and Evans 1954; Salthaug and Aanes 2003). The index of spatial patchiness used here is the coefficient of dispersion, which measures the degree of dispersion of E within a trip (FT_PATCH) or within a year (YE_PATCH).

$$\text{(6)}\qquad \text{FT\_PATCH}_{v,i} = \frac{s^2_{v,i}}{\mu_{v,i}}$$

$$\text{(7)}\qquad \text{YE\_PATCH}_{v,y} = \frac{s^2_{v,y}}{\mu_{v,y}}$$

where $s^2_{v,i}$ and $\mu_{v,i}$ are the variance and mean of E calculated over all the statistical rectangles visited by vessel v during trip i; $s^2_{v,y}$ and $\mu_{v,y}$ are the respective values for year y. Values of FT_PATCH and YE_PATCH larger than 1 indicate an increasingly patchy distribution, whereas values lower than 1 reflect increasingly uniform distributions. Values of 0 reflect a fully uniform distribution. Values of 1 indicate that the distribution is random.

Annual index of intra-annual consistency

This index, which to our best knowledge is not referred to in the fisheries literature, describes how traditional or how exploratory skippers have been during a fishing trip or year. It has been included here to characterize the ability of a skipper to change a fishing pattern from one fishing trip to another. It is calculated as the difference between each fishing pattern of each fishing trip and the average fishing pattern observed over the year, scaled by the number of trips and the number of rectangles visited. This index reflects a fishing strategy, but it cannot be adapted to characterize fishing tactics.

$$\text{(8)}\qquad \text{YE\_IAC}_{v,y} = \frac{1}{AI} \sum_{i=1}^{I} \sum_{a=1}^{A} \left(\frac{\text{En}_{v,i,a}}{\text{En}_{v,i,A}} - \frac{\text{En}_{v,y,a}}{\text{En}_{v,y,A}} \right)^2$$

Low values of YE_IAC indicate that skippers keep a similar fishing pattern from one trip to another. High values of YE_IAC indicate that skippers have an exploratory or opportunistic behavior.

Modelling catch rates

Catch rates (CPUE, catch per unit effort) calculated for each vessel and fishing trip are modeled using GLMs (McCullagh and Nelder 1989). The distribution of CPUE is

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first examined to identify and eliminate outliers. Then, to model catch rates, it is necessary to select a probabilistic distribution. CPUE are typically positive, skewed, continuous variables, which could typically be modeled using any of the gamma, inverse Gaussian, or log-normal distributions (McCullagh and Nelder 1989). However, to obtain additive effects, we consider only the gamma and the log-normal distributions. It is possible to obtain additive effects with the gamma distribution by choosing a logarithmic link function. If CPUE are log-normally distributed, it is possible to obtain additive effects by log-transforming CPUE (log CPUE will be normally distributed) and simply choose the identity link function. To choose between these two stochastic models, the distribution of CPUE is tested visually against a gamma distribution, using QQ plots, and the distribution of log CPUE is similarly tested against a normal distribution. The most appropriate combination of explained variable and probability distribution (CPUE – gamma distribution (model type 1) or log-transformed CPUE – normal distribution (model type 2)) is selected. The link function is either Logarithm (model type 1) or Identity (model type 2).

The explanatory variables are year, métier (class variables), and the different indices of fishing tactics or strategies defined above (continuous variables). The year effect may quantify a combination of annual abundance changes and technical creeping. Each observation cell is a combination of vessel and fishing trip. One complete analysis is carried out for each fleet and each species examined. A general formulation of the model is

(9*a*) Model 1:

$$\ln(\overline{\mathrm{CPUE}}) = \hat{\alpha} + \hat{\beta}_y + \hat{\gamma}_m + \sum_{k=1}^{NI} \hat{\theta}_k \mathbf{INDEX}_k$$

(9*b*) Model 2:

$$\overline{\ln(\mathrm{CPUE})} = \hat{\alpha} + \hat{\beta}_y + \hat{\gamma}_m + \sum_{k=1}^{NI} \hat{\theta}_k \mathbf{INDEX}_k$$

where α is the intercept, β is the year effect, γ is the métier effect, θ_k is the regression coefficient associated with $\mathbf{INDEX}_k$, and $\mathbf{INDEX}_k$ is the vector of selected indices of tactics or strategies.

The antilogarithmic transformation of model 1 is straightforward:

(10*a*) Model 1:

$$\overline{\mathrm{CPUE}} = \exp\left(\hat{\alpha} + \hat{\beta}_y + \hat{\gamma}_m + \sum_{k=1}^{NI} \hat{\theta}_k \mathbf{INDEX}_k\right)$$

The antilogarithmic transformation of model 2 requires a correction for bias using the factor $\exp(\sigma^2/2)$, where σ is the standard error of the estimate of log(CPUE):

(10*b*) Model 2:

$$\overline{\mathrm{CPUE}} = \exp\left(\hat{\alpha} + \hat{\beta}_y + \hat{\gamma}_m + \sum_{k=1}^{NI} \hat{\theta}_k \mathbf{INDEX}_k - \frac{\sigma^2}{2}\right)$$

Nevertheless, if the fit of model 2 is reasonable, then σ^2 is small and the bias induced by the antilogarithmic transformation can be ignored. The estimate of CPUE under model 2 may then be simply expressed by eq. 10*a*.

The model is preliminarily parameterized using the outcomes of the data exploration, which allows to select the final observation set (elimination of outliers), to select a preliminary set of candidate explanatory variables, and to choose the a priori, most appropriate model type (1 or 2). The model chosen is validated with regards to residual plots resulting from the analysis. Residuals are plotted against predicted values and are tested visually for normal distribution (QQ plot). Once an appropriate model type (1 or 2) is selected, the goodness of fit of the model is evaluated using the model's scaled deviance and Pearson χ^2 and two other criteria: Akaike's Information Criterion (AIC) and the Schwarz Bayesian Information Criterion (BIC). If the model chosen fits reasonably well the data, both AIC and BIC should be as low as possible. In addition, both scaled deviance and Pearson χ^2 should have a χ^2 distribution, with degrees of freedom equal to the number of observations minus the number of parameters estimated. It follows that the ratio between scaled deviance and degrees of freedom and also the ratio between Pearson χ^2 and degrees of freedom should be close to 1. Finally, only the most contributive explanatory variables are retained in the final model (Type III analysis).

Adjusting *E*

The method is adapted from the traditional approach (Gulland 1964; Robson 1966; Kimura 1981). The adjustment factors are the métier effect and the coefficients associated to the indices of fishing tactics or strategies as estimated by eqs. 9 and 10, when the goodness of fit of the model is reasonable and when σ^2 may be subsequently neglected. If γ_o is the effect of the reference métier, the relationship between the adjusted (or effective) log fishing effort (ln_Ee) and the nominal (or untransformed) log fishing effort (ln_En) may be expressed as

$$(11a) \quad \ln\_Ee_{y,j} = \ln\_En_{y,j} + (\hat{\gamma}_m - \hat{\gamma}_o) + \sum_{k=1}^{NI} \hat{\theta}_k \mathbf{INDEX}_{k,y,j}$$

Similarly, the relationship between the adjusted (or effective) Ee and the nominal (or untransformed) En may be expressed as

$$(11b) \quad Ee_{y,j} = En_{y,j} \exp\left[(\hat{\gamma}_m - \hat{\gamma}_o) + \sum_{k=1}^{NI} \hat{\theta}_k \mathbf{INDEX}_{k,y,j}\right]$$

Evaluating the benefits of adjusting *E*

The benefits of adjusting *E* are evaluated by scrutinizing the relationship between *F* and *E*, where effort is defined as either nominal or adjusted effort. Partial *F* was calculated for each combination of fishing vessel and fishing trip by weighting the total *F* using the ratio of the vessel's and trip's landings to the total international landings for the stock under consideration. The relationship between *F* and effort was examined for the main stocks harvested by the fleets under investigation and for which a stock assessment was avail-

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able. If q represents the catchability coefficient, the relationship between partial F and E may be expressed as

$$F_{v,i} = q\,E_{v,i}$$

The scope of this analysis is to compare the goodness of fit of the relationship between F and En (eq. 12*a*) with the goodness of fit of the relationship between F and Ee (eq. 12*b*):

$$(12a) \quad F_{v,i} = q\,\mathrm{En}_{v,i}$$

$$(12b) \quad F_{v,i} = q\,\mathrm{Ee}_{v,i} = q\,\mathrm{En}_{v,i} \times \exp\left[(\hat{\gamma}_m - \hat{\gamma}_o) + \sum_{k=1}^{NI} \hat{\theta}_k\,\mathbf{INDEX}_{k,v,i}\right]$$

The comparison between eqs. 12*a* and 12*b* will be carried out in two ways. First, a simple no-intercept linear regression between F and effort will be tested with effort defined as nominal or adjusted. Second, a linear regression between log-transformed F and effort will be tested with effort defined as nominal or adjusted. For both approaches, the goodness of fit of the regressions will be appraised by (*i*) eye-balling the plots between F and effort (or log(F) and log(effort)) and (*ii*) comparing the values of R^2. In addition, for the second approach, a t test has been applied to test the value of the regression slope, which should be close to 1 if the regression model (eq. 12*b*) is appropriate.

The methods developed in this study were implemented using SAS/STAT (SAS Institute Inc. 1999). In particular, procedure GENMOD was used to implement the GLMs.

Results

Fishing tactics

The indices of fishing tactics FT_SW, FT_DIST, and FT_PATCH appeared to vary substantially from one fishing vessel and trip to another (Fig. 2). The maximum number of rectangles visited during a trip was on average two (FT_SW < ln(2)) for the Danish, English, and Dutch fleets; three for the Basque fleets (ln(2) < FT_SW < ln(3)); and five for the French fleets (ln(4) < FT_SW < ln(5)). FT_SW and FT_DIST generally appeared to increase with vessel length and horsepower within the same stratum country × harbor × main gear (e.g., Danish gill-netters, Danish seiners, Danish otter trawlers, Dutch beam trawlers; Fig. 2). The low value of FT_PATCH for the Danish, English, and Dutch fleets resulted from few rectangles (<2) visited and not from the spatial distribution of E being scattered. FT_PATCH could therefore not be used to reflect appropriately the patchiness of effort distribution, and it was not retained as an explanatory variable in subsequent analyses relative to these fleets. Given that the number of rectangles visited for the French and Basque fleets was on average higher than three, the value of FT_PATCH could be interpreted to characterize the spatial distribution of E. FT_PATCH was much higher than one for these fleets, suggesting a patchy distribution of E during fishing trips. The weighted distance between rectangles visited during a fishing trip (FT_DIST) is strongly correlated to FT_SW, while FT_PATCH was generally negatively correlated with FT_SW (Fig. 3).

Fishing strategies

The number of ICES rectangles visited during a year (reflected by YE_SW) is much higher than that visited during one fishing trip (reflected by FT_SW) for all fleets (Fig. 2). This observation indicates shifts in fishing tactics from one fishing trip to another. The weighted distance between rectangles visited during a year (YE_DIST) is strongly correlated to YE_SW (Fig. 3). YE_PATCH was generally much higher than one, indicating patchy distributions, and was negatively correlated with YE_SW. A maximum of two métiers was carried out by each vessel of most fleets during 1 year (YE_SW_METIER < ln(2)). The vessels of fleets FL09 and FL12, however, could carry out a maximum of three métiers throughout the year. Métier shifts (as reflected by YE_METIER) were not consistently correlated with the other indices. Intra-annual shifts in fishing tactics, as reflected by YE_IAC, were not consistently correlated with YE_SW. The inter-annual variations in the different indices of fishing tactics and strategies were generally negligible, and these have not been represented here.

CPUE analysis outputs

The statistics resulting from the application of GLMs to the different combination of fleets and species are summarized (Table 4). Results are only presented for the 43 combinations of fleets and species where an appropriate model could be fitted. The métier effect (Figs. 4, 5, and 6) was significant ($p < 0.0001$) for all combinations of fleets and species under examination.

Considering fleets FL01–FL04 (gill-netters), the highest catch rates of European plaice (*Pleuronectes platessa*), common sole (*Solea solea*), and Atlantic cod (*Gadus morhua*) are reached with nets configured for fishing these species. In fleets FL05–FL08 (Danish seiners and otter trawlers), European plaice appears to be the main target species in the North Sea, while the main target species in other areas (Skagerrak, Western Baltic Sea) is Atlantic cod. For fleet FL09 (English otter trawlers), Atlanic cod and haddock (*Melanogrammus aeglefinus*) fishing activities can hardly be distinguished using the current definition of métiers. In fleets FL10, FL13, and FL14 (beam trawlers), the highest catch rates are achieved with a mesh size of 80 mm for common sole fishing. With respect to European plaice fishing, the highest catch rates are reached when the mesh size range is of 100–134 mm for the Dutch large beam trawlers (FL14). The relationship between mesh size and European plaice CPUE is more complex for the small Dutch beam trawlers (FL13). For fleets FL11–FL12 (French large otter trawlers), the highest CPUE of Atlantic cod and whiting (*Merlangius merlangus*) are achieved in the Celtic Sea with a mesh size of 100 mm. Atlantic cod and whiting fishing activities cannot be distinguished using the current definition of métiers. With respect to saithe (pollock, *Pollachius virens*) fishing, the most appropriate mesh size is of 110 mm (FL11) and 100 mm (FL12), irrespective of the fishing ground visited. The relationship between CPUE and mesh size is unclear and (or) area-dependent for the other species (anglerfish, blue ling, roundnose grenadier, black scabbardfish). Highest CPUE of blue ling, roundnose grenadier, and black scabbardfish are associated with ICES divisions VIa (Western Scottish waters) and VII (Celtic Sea). For fleets FL15–FL17

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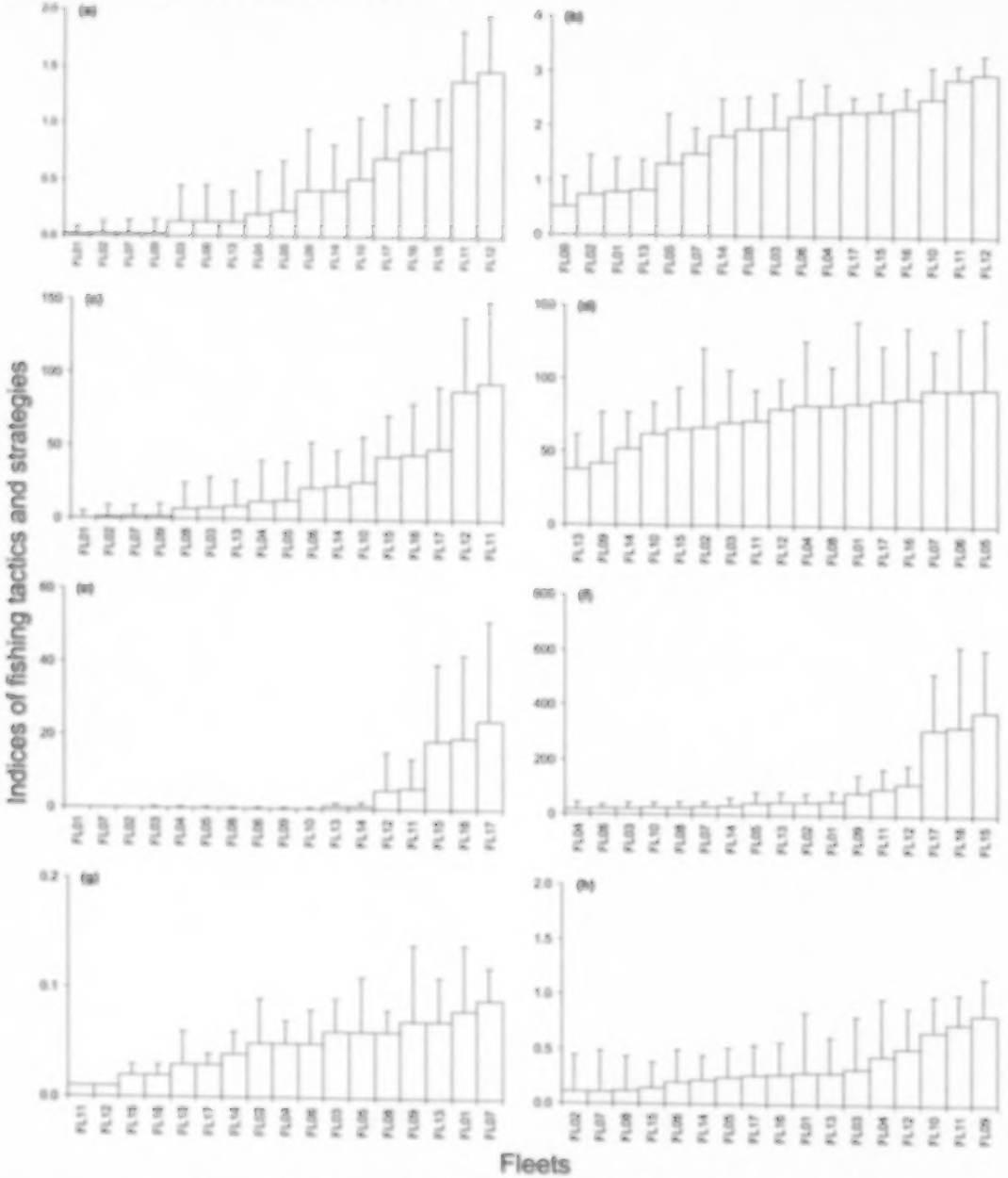
Fig. 2. Average value and standard deviation of the indices of fishing tactics and fishing strategies, sorted in ascending order, for the fleets under investigation. (*a*) FT_SW, (*b*) YE_SW, (*c*) FT_DIST, (*d*) YE_DIST, (*e*) FT_PATCH, (*f*) YE_PATCH, (*g*) YE_IAC, (*h*) YE_SW_METIER. See Table 4 for definitions of these indices.



(Basque otter trawlers), catch rates are the highest for pair trawlers and "Baka" otter trawlers operating in sub-area VII, with respect to the European hake fishery. With respect to anglerfish fishing, the highest catch rates are achieved in sub-area VII for fleet FL16 and in sub-area VIII for fleet FL17.

The effects of the different indices of fishing tactics and strategies on CPUE are shown (Table 4; Figs. 7 and 8). The most influential indices are the Shannon–Wiener spatial diversity indices FT_SW and YE_SW and, to a lower extent, YE_DIST and YE_IAC. The effect of YE_DIST on catch rates was lower than –0.5 in two cases: FL08 fishing European plaice and FL12 fishing whiting. The effect of YE_IAC on catch rates was higher than 0.5 for fleet FL07 fishing European plaice and lower than –0.5 for fleet FL11 fishing saithe. The other indices (FT_DIST, FT_PATCH,

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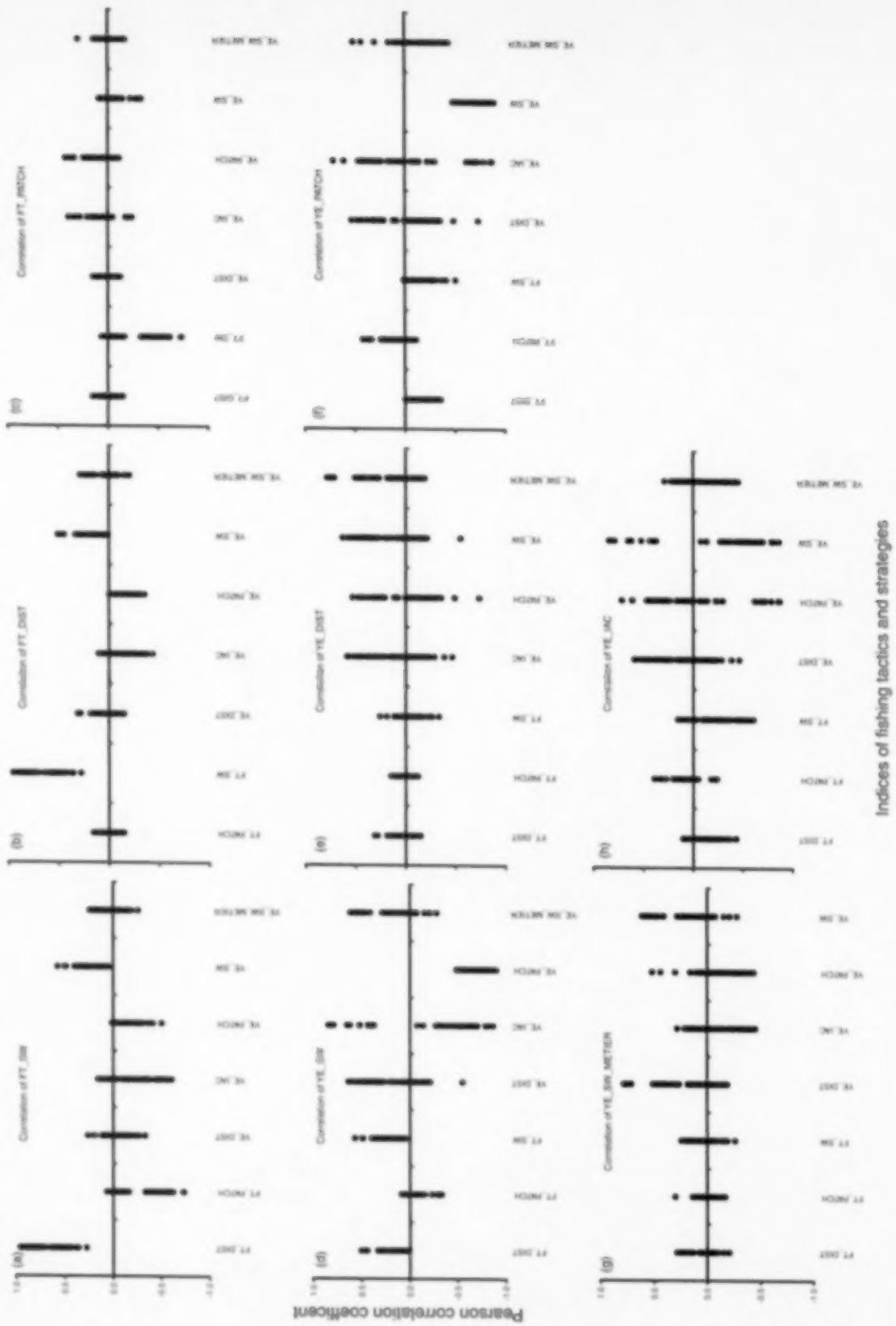

Fig. 3. Pearson's correlation coefficients calculated between (*a*) FT_SW, (*b*) FT_DIST, (*c*) FT_PATCH, (*d*) YE_SW, (*e*) YE_DIST, (*f*) YE_PATCH, (*g*) YE_SW_METIER, (*h*) YE_IAC and the other indices of fishing tactics and strategies for all the fleets under investigation. See Table 4 for definitions of these indices.

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Table 4. Summary of the statistics assessing the goodness of fit of the generalized linear models applied to each combination of country, fleet, and species.

Country	Fleet	Species[a]	Model type	DF	SCD/DF	SCC/DF	FT_SW	FT_DIST	FT_PATCH	YE_DIST
Denmark	FL01	Atlantic cod	2	4 011	1.00	1.00				×
		European plaice	2	3 614	1.00	1.00				
		Common sole	2	1 913	1.01	1.01				×
	FL02	Atlantic cod	2	5 746	1.00	1.00				×
		European plaice	2	4 958	1.00	1.00				
		Common sole	2	2 428	1.01	1.01				×
	FL03	Atlantic cod	2	5 819	1.00	1.00	×			
		European plaice	2	4 321	1.00	1.00				×
		Common sole	2	2 619	1.00	1.00				
	FL04	Atlantic cod	1	4 303	1.10	0.83	×			×
		European plaice	2	2 505	1.00	1.00				×
		Common sole	2	1 564	1.01	1.01				
	FL05	Atlantic cod	2	1 108	1.01	1.01	×			
		European plaice	1	1 111	1.17	0.94	×			
	FL06	Atlantic cod	1	4 406	1.16	1.10	×			
		European plaice	2	4 210	1.00	1.00	×			
	FL07	Atlantic cod	2	4 260	1.00	1.00				
		European plaice	2	4 329	1.00	1.00				
	FL08	Atlantic cod	2	4 886	1.00	1.00				×
		European plaice	2	4 213	1.00	1.00				×
England	FL09	Atlantic cod	2	45 651	1.00	1.00				
		Haddock	2	31 952	1.00	1.00				
	FL10	European plaice	1	7 268	1.04	0.97	×			
		Common sole	2	4 153	1.00	1.00	×			
France	FL11	Blue ling	2	1 121	1.02	1.02	×	×		
		Black scabbardfish	2	842	1.02	1.02		×	×	
		Saithe	2	1 085	1.02	1.02	×		×	×
		Roundnose grenadier	2	853	1.03	1.03	×		×	
	FL12	Blue ling	2	2 983	1.01	1.01	×		×	
		Black scabbardfish	2	3 151	1.01	1.01	×	×		
		Atlantic cod	2	3 341	1.01	1.01	×	×	×	
		Anglerfish	2	4 207	1.01	1.01	×	×	×	
		Saithe	2	3 170	1.01	1.01	×		×	×
		Roundnose grenadier	2	3 064	1.01	1.01	×		×	×
		Whiting	2	2 114	1.02	1.01	×			×
Netherlands	FL13	European plaice	2	2 960	1.00	1.00				
		Common sole	1	3 338	1.06	0.93				
	FL14	European plaice	1	44 108	1.06	1.04				
		Common sole	1	50 012	1.06	1.01				
Spain	FL15	European hake	1	2 616	1.09	1.57				×
	FL16	European hake	1	3 175	1.09	1.49				
	FL17	European hake	1	2 618	1.09	1.26				×
		Anglerfish	1	1 715	1.08	1.52				×

Note: Model type (1, gamma distribution – logarithmic link function; 2, normal distribution – identity link function); DF, degrees of freedom; SCD/DF, Pearson χ^2 to DF; FT, fishing tactic index; YE, fishing strategy index; SW, Shannon–Wiener spatial diversity index; DIST, efforts-weighted average of all (tactics index FT_DIST) or one year (strategy index YE_DIST); PATCH, degree of dispersion (patchiness) of fishing effort within a trip (FT_PATCH) or annual consistency, which characterizes the ability of a skipper to change a fishing pattern from one fishing trip to another; METIER, annual index of mobile skippers have been with regards to the number of métiers selected during a year. An × indicates where an explanatory variable is significant significant ($p < 0.05$).

[a]Anglerfish (*Lophius* spp.), black scabbardfish (*Aphanopus carbo*), blue ling (*Molva dypterygia*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus plaice* (*Pleuronectes platessa*), roundnose grenadier (*Coryphaenoides rupestris*), saithe (pollock, *Pollachius virens*), common sole (*Solea solea*), whiting

YE_PATCH, YE_SW_METIER) had a lesser impact on catch rates (the estimated coefficients are included in the range –0.5 to 0.5).

FT_SW is always negatively correlated with the CPUE of any combination of fleet and species. YE_SW allows discrimination between mobile (high YE_SW) and stationary (low YE_SW) fishing strategies. The benefits of pursuing a mobile or a stationary fishing strategy are clearly case dependent. Of the 43 combinations of fleets and species investigated, YE_SW was positively correlated to catch rates 21 times, negatively correlated to catch rates 13 times, and not significant 9 times. The nature of the linkage between fishing strategies and catch rates generally does not appear to be clearly gear or species dependent. For instance, with

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fleet, and species.

YE_IAC	YE_PATCH	YE_SW	YE_SW_METIER
×			
		×	
×		×	
×			
		×	
×		×	
			×
×	×	×	
			×
×		×	
		×	×
×		×	
×		×	
×			
		×	
×			×
×	×	×	
		×	
	×	×	
		×	
×		×	
×		×	
		×	
	×	×	
×	×	×	
×	×	×	
	×	×	×
×		×	×
		×	×
×	×	×	×
		×	
×	×	×	×
		×	×
×		×	
×			
×		×	
×		×	
×		×	
		×	×
×			
×		×	

ratio of scaled deviance to DF; SCC/DF, ratio of scaled distances between fishing areas visited within one fishing trip within a year (YE_PATCH); IAC, annual index of intra-métier diversity, which describes how stationary or how ($p < 0.05$). The métier and the year effects were always

aeglefinus), European hake (*Merluccius merluccius*), European (*Merlangius merlangus*).

regards to the flatfish fishery, pursuing a mobile strategy appears to be attractive (YE_SW > 0) for fleets FL01 and FL10, but not for fleet FL14. Such contrasted results are also observed for the fisheries harvesting Atlantic cod, anglerfish, blue ling, and black scabbardfish. For both fleets FL11 and FL12, vessels pursuing a more mobile strategy have the highest catch rates of roundnose grenadier. Overall, the impact on catch rates of fishing strategies (as reflected by YE_SW) appears to be of a more complex nature than that of fishing tactics (as reflected by FT_SW).

Having examined the respective effect of métier choices and of the different indices of fishing tactics and strategies, we examined the relative contribution of each factor to catch-rate variations. In most cases, the métier effect appeared to be dominant. This is illustrated for selected combinations of fleets and species (Fig. 9). In these examples, the métier effect clearly discriminates catch rates for fleets FL04 fishing European plaice and common sole, FL09 fishing Atlantic cod, FL10 fishing common sole, FL11 fishing saithe, and FL15 fishing European hake. For these combinations, catch rates are reasonably correlated with the other components of fishing power (indices of fishing tactics and strategies) within each important métier stratum.

Relationship between *E* and *F*

The relationship between E and F and also the relationship between $\log(E)$ and $\log(F)$ were investigated in situations where a stock assessment was available (i.e., 38 combinations of fleets and stocks). Adjusting E led to a substantial increase in the R^2 of the regression between F and E, except for fleets FL08 harvesting North Sea Euroopean plaice, FL09 harvesting North Sea Atlantic cod, and FL17 harvesting Celtic Sea – Bay of Biscay anglerfish (Table 5). In all but one case (FL05 fishing North Sea Atlantic cod), adjusting E led to a substantial improvement of the relationship between $\log(F)$ and $\log(E)$ (Table 6; Figs. 10 and 11). The average slope of the regression with log(Ee) was in the range 0.95–1.05 for 15 of the combinations of fleets and stocks, and it was not significantly different from 1 for 11 of these combinations. For these 11 combinations, the traditional assumption that F is directly proportional to Ee is reasonable, provided E has been adjusted using the skipper effect. For the other combinations, adjusting E generally leads to a substantial improvement of the relationship between F and E. However, F is not directly proportional to Ee.

Discussion

The three objectives of this study were (*i*) to characterize and quantify, using a set of descriptive variables, shifts in fishing tactics and strategies for a wide spectrum of European fleets, (*ii*) to evaluate the extent to which these variables may be used to model catch rates, and (*iii*) to assess the benefits of adjusting E with the coefficients derived from the analysis (*ii*).

The fishing tactics index FT_SW describes the fishermen's mobility at the scale of a fishing trip, while the fishing strategy YE_SW features the same aspects at the scale of the year. FT_SW and YE_SW increased with vessel length and horsepower, which could be anticipated, since larger vessels have in principle the potential for exploring more rectangles. Catch rates were strongly correlated to métier choices and to the indices FT_SW and YE_SW. In particular, FT_SW was negatively correlated to the catch rates of each combination of fleets and species investigated. This result was expected for two main reasons. First, because fishing vessels search for fish aggregations, their catchability is anticipated to increase when the area occupied by the stock decreases. Given

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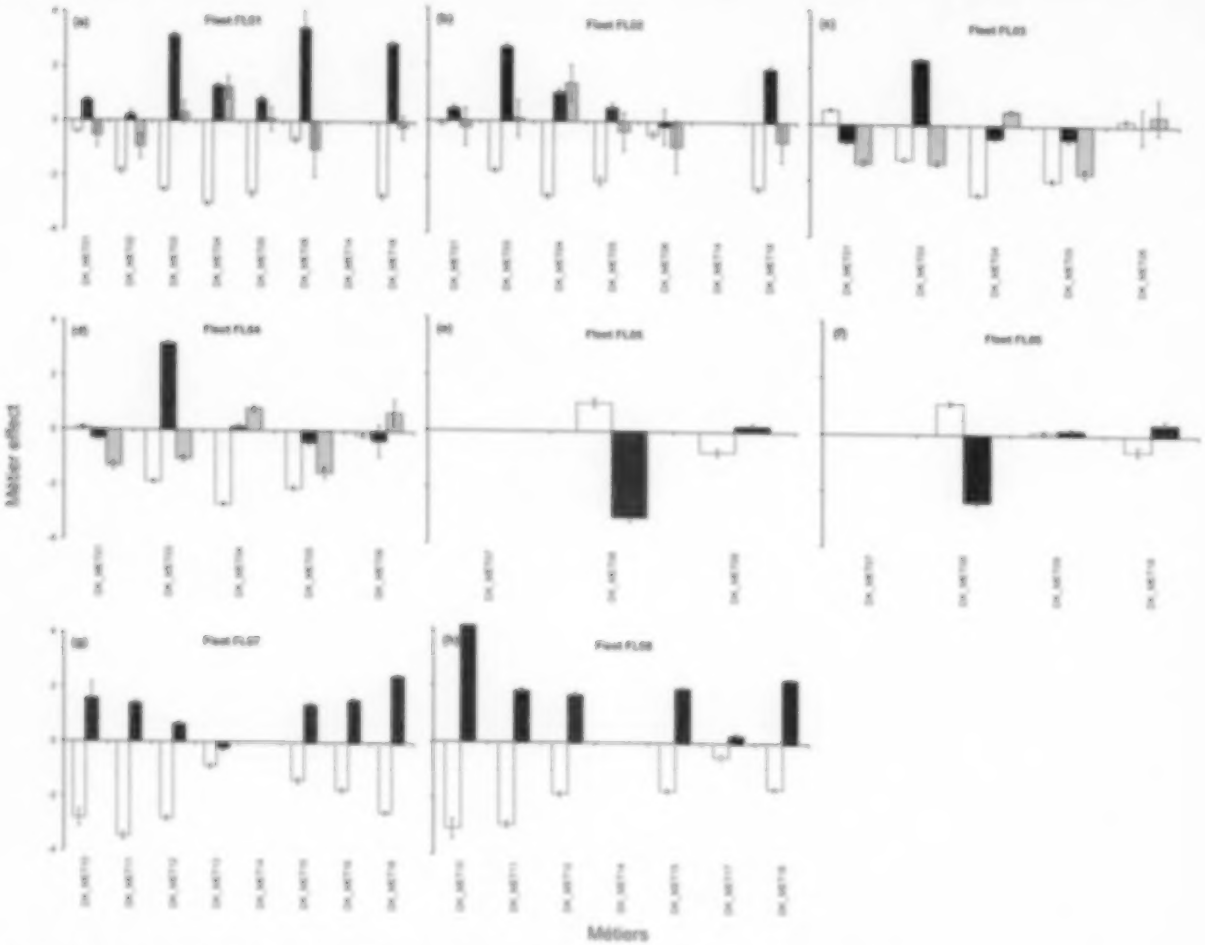
Fig. 4. Effects of the different métiers as derived from the generalized linear models. Data shown are for Danish (DK) fleets (FL01–FL08) harvesting Atlantic cod (*Gadus morhua*, open bars); European plaice (*Pleuronectes platessa*, solid bars); and common sole (*Solea solea*, shaded bars).



that the spatial distribution of the fleet gives an indication of the area occupied by the targeted population, vessels of limited spatial distribution within a trip have the highest catchability. Second, FT_SW quantifies to some extent the ability of skippers to locate high fish densities during a fishing trip. One may anticipate that during a fishing trip, vessels with high FT_SW have been searching fish aggregations for a long time, while vessels with low FT_SW have been more efficient in finding and subsequently harvesting these aggregations. These results bear out the findings of Salthaug and Aanes (2003), who investigated the linkage between catch rates and the distribution of fishing effort deployed by the Norwegian fleets harvesting gadoids in the North Sea and the Barents Sea. FT_SW appears to be a reasonable candidate to quantify the skipper's effect during a fishing trip.

The influence of fishing strategies on catch rates was of a more complex nature. Depending on the combination of fleet and species, YE_SW was positively or negatively correlated to the catch rates. One may anticipate that there was little benefit in visiting many fishing grounds for the vessels and fisheries where negative correlation was found. The vessels pursuing such a stationary strategy are referred to by Hilborn (1985) as "area-specialists". These vessels specialize in a particular area and learn everything possible about catching fish in that area. For other vessels and fisheries, a broad distribution of fishing effort proved to be an appropriate strategy to promote high yields. These results bear out those of Abrahams and Healey (1990), who found that mobile vessels had the highest catch rates of sockeye salmon (*Oncorhynchus nerka*). Such vessels, which are referred to by Hilborn (1985) as "movement-specialists", are reputed to develop skills appropriate to any area and then to fish opportunistically in a large number of different areas to maximize catch rates. In addition, stationary strategies could lead to local depletion for nonresilient species, thereby adversely impacting catch rates (Rijnsdorp et al. 2000*a*). Both interpretations may explain why French vessels pursuing a mobile strategy have the highest catch rates of roundnose grenadier, which is a nonresilient species and the commer-

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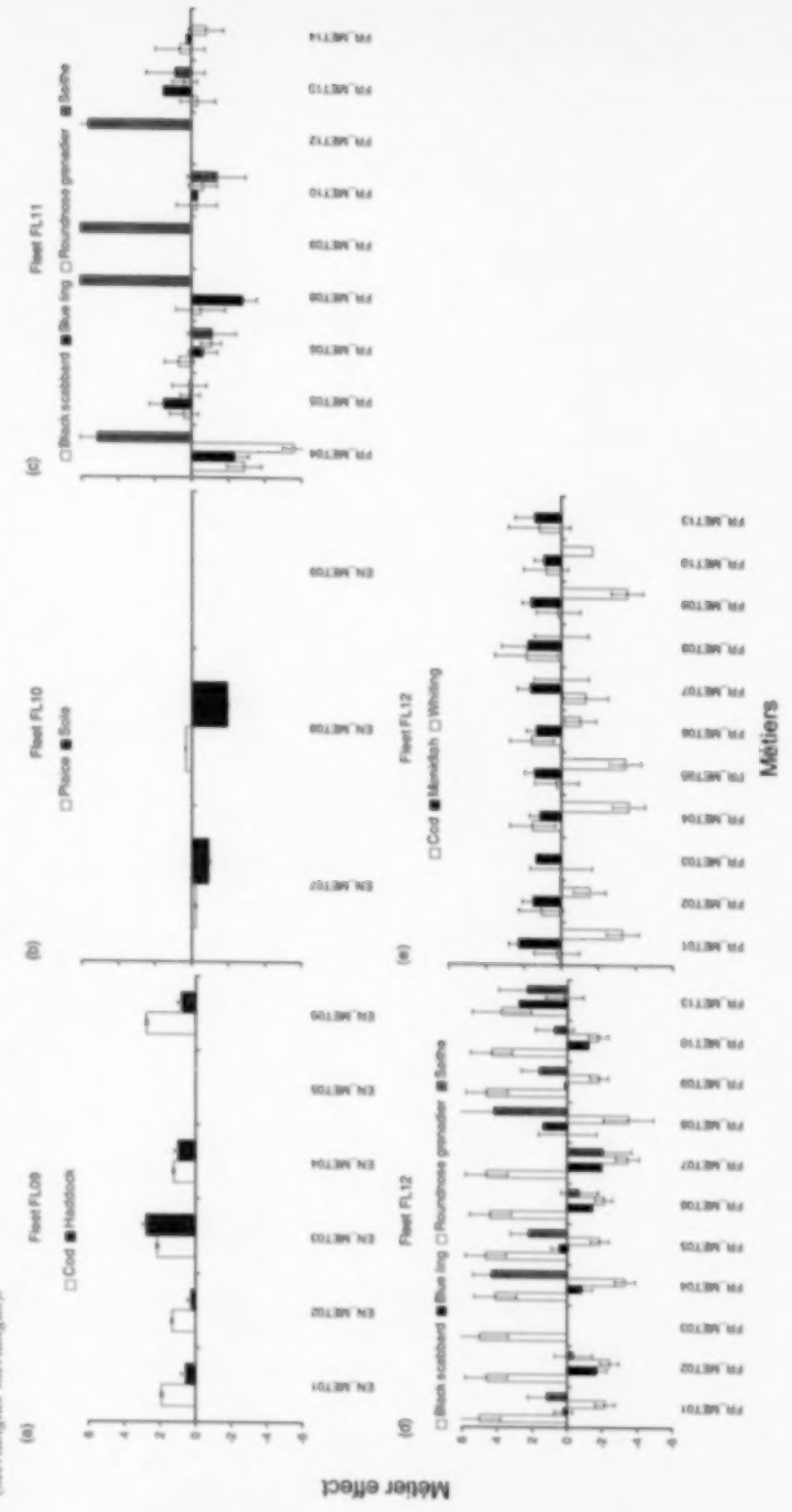

Fig. 5. Effects of the different métiers as derived from the generalized linear models. Data shown are for English (EN) and French (FR) fleets (FL09–FL12) harvesting anglerfish (monkfish, *Lophius* spp.), black scabbardfish (*Aphanopus carbo*), blue ling (*Molva dypterigia*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), European plaice (*Pleuronectes platessa*), roundnose grenadier (*Coryphaenoides rupestris*), saithe (pollock, *Pollachius virens*), common sole (*Solea solea*), and whiting (*Merlangius merlangus*).

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Fig. 6. Effects of the different métiers as derived from the generalized linear models. Data shown are for Dutch (NL) and Basque (BC) fleets (FL13–FL17) harvesting anglerfish (*Lophius* spp., shaded), European hake (*Merluccius merluccius*, hatched bars), European plaice (*Pleuronectes platessa*, open bars), and common sole (*Solea solea*, solid bars).

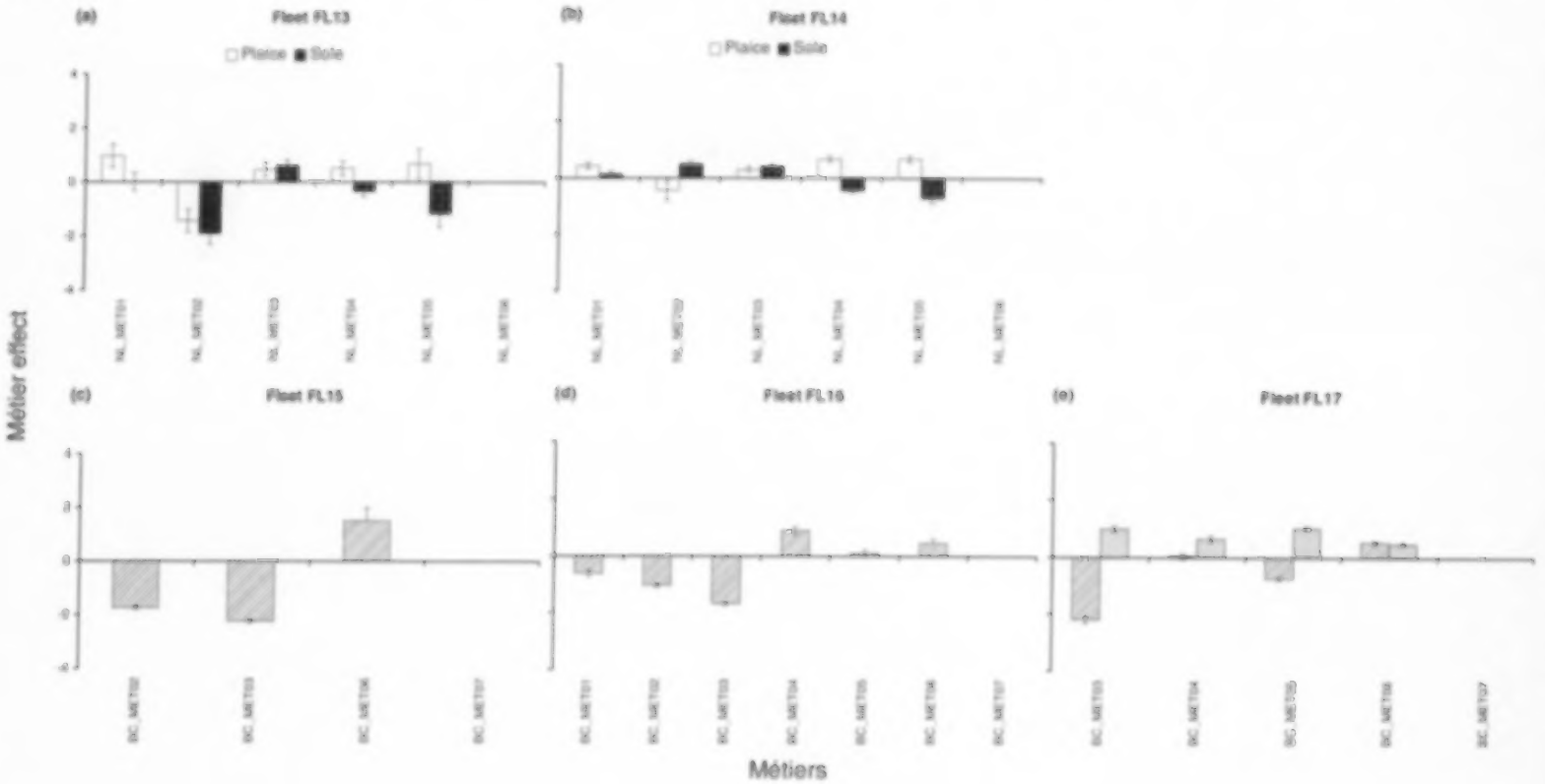

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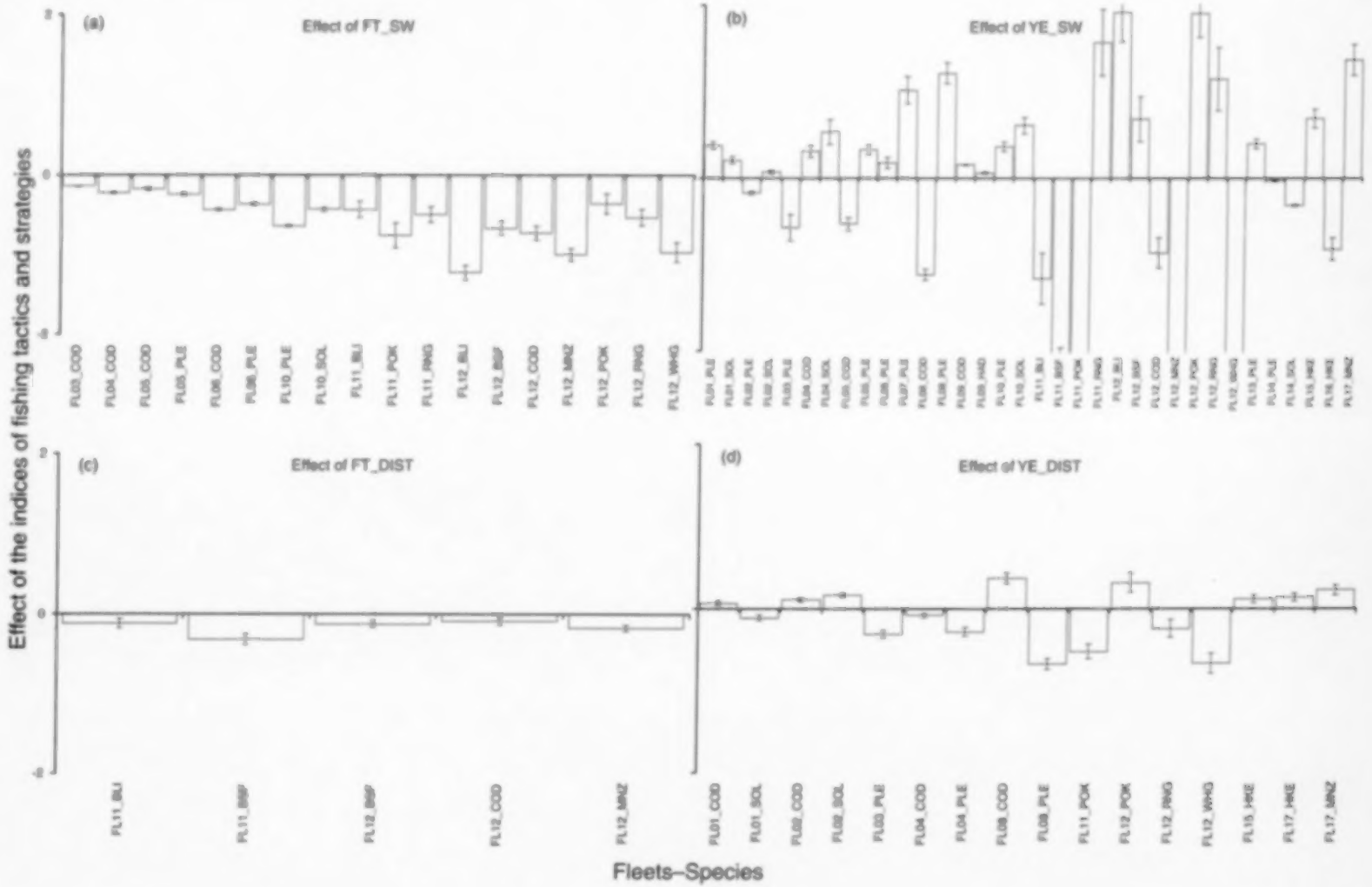
Fig. 7. Effects of the indices of fishing tactics FT_SW (*a*) and FT_DIST (*c*) and strategies YE_SW (*b*) and YE_DIST (*d*), as derived from the generalized linear models, for the different combinations of fleets and species. See Table 4 for definitions of these indices. BLI, blue ling (*Molva dypterygia*); BSF, black scabbardfish (*Aphanopus carbo*); COD, Atlantic cod (*Gadus morhua*); HAD, haddock (*Melanogrammus aeglefinus*); HKE: European hake (*Merluccius merluccius*); MNZ, anglerfish (*Lophius* spp.); PLE, European plaice (*Pleuronectes platessa*); POK, saithe (pollock, *Pollachius virens*); SOL, common sole (*Solea solea*); WHG, whiting (*Merlangius merlangus*).



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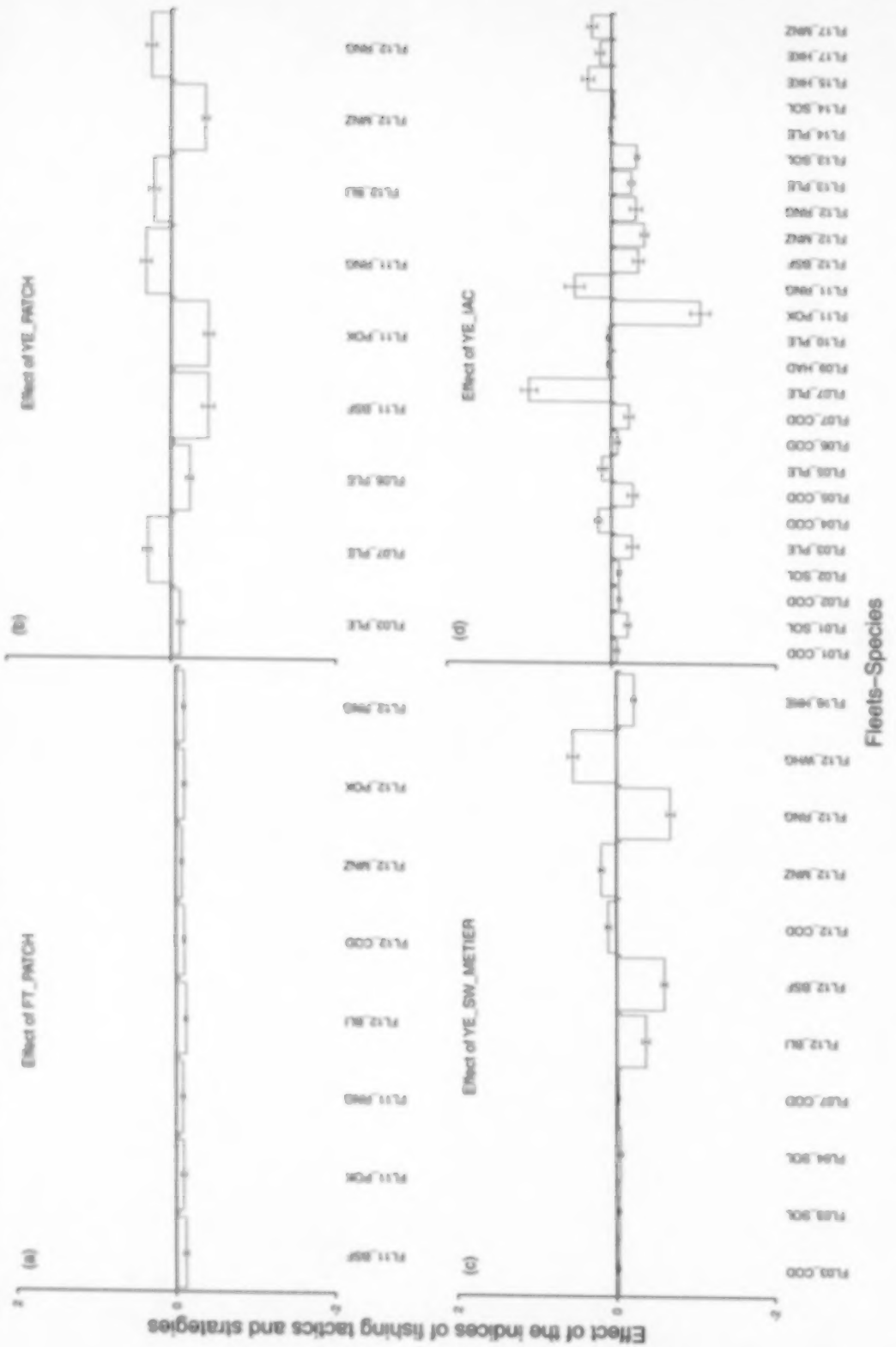

Fig. 8. Effects of the indices of fishing tactics FT_PATCH (*a*) and strategies YE_PATCH (*b*), YE_SW_METIER (*c*), and YE_IAC (*d*), as derived from the generalized linear models, for the different combinations of fleets and species. See Table 4 for definitions of these indices. BLI, blue ling (*Molva dypterygia*); BSF, black scabbardfish (*Aphanopus carbo*); COD, Atlantic cod (*Gadus morhua*); HAD, haddock (*Melanogrammus aeglefinus*); HKE, European hake (*Merluccius merluccius*); MNZ, anglerfish (*Lophius* spp.); PLE, European plaice (*Pleuronectes platessa*); POK, saithe (pollock, *Pollachius virens*); SOL, common sole (*Solea solea*); WHG, whiting (*Merlangius merlangus*).

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Fig. 9. Relationships between log-transformed catch per unit effort (CPUE) and fishing power by métier as derived from the generalized linear models. Data shown are for fleets FL04 harvesting European plaice (*Pleuronectes platessa*) (*a*) and common sole (*Solea solea*) (*b*), FL09 harvesting Atlantic cod (*Gadus morhua*) (*c*), FL10 harvesting common sole (*d*), FL11 harvesting saithe (pollock, *Pollachius virens*) (*e*), and FL15 harvesting European hake (*Merluccius merluccius*) (*f*). DK, Denmark; EN, England; FR, France; BC, Basque Country.

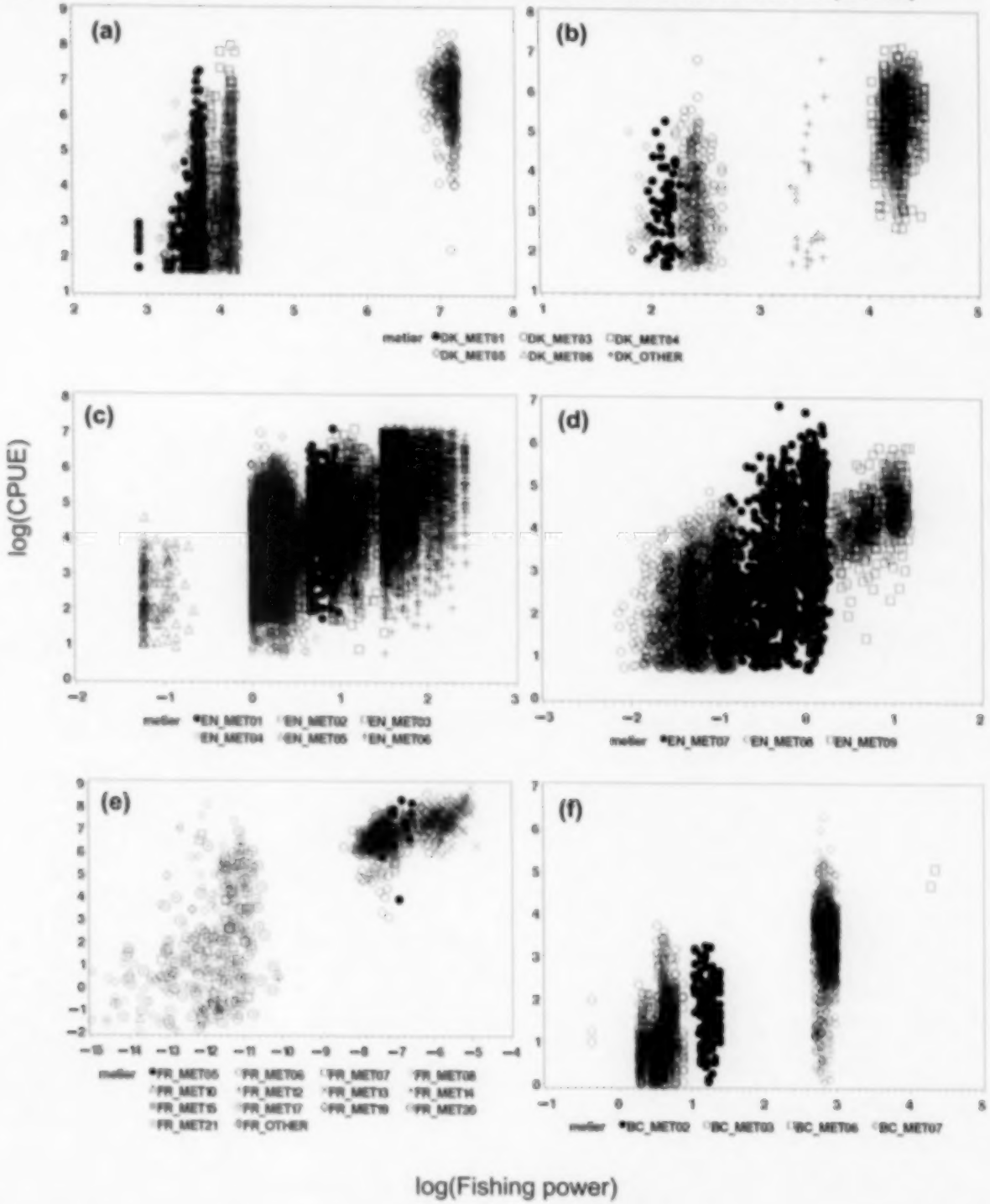

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Table 5. Output comparison of (*a*) the no-intercept regression between fishing mortality (*F*) and nominal fishing effort (En) and (*b*) the no-intercept regression between fishing mortality (*F*) and adjusted fishing effort (Ee).

Fleet	Stock	*N*	R^2 (*a*)	R^2 (*b*)	Equation (*b*)
FL01	NS Atlantic cod	1 970	0.43	0.54	$F = 5.80 \times 10^{-5} \times Ee$
	NS European plaice	2 200	0.35	0.49	$F = 1.43 \times 10^{-7} \times Ee$
	NS common sole	1 279	0.40	0.50	$F = 1.19 \times 10^{-4} \times Ee$
FL02	NS Atlantic cod	3 003	0.37	0.49	$F = 4.29 \times 10^{-5} \times Ee$
	NS European plaice	2 495	0.40	0.56	$F = 7.99 \times 10^{-6} \times Ee$
	NS common sole	1 216	0.39	0.47	$F = 1.97 \times 10^{-5} \times Ee$
FL03	NS Atlantic cod	1 089	0.54	0.71	$F = 4.58 \times 10^{-5} \times Ee$
	NS European plaice	3 346	0.24	0.56	$F = 5.58 \times 10^{-6} \times Ee$
	NS common sole	1 972	0.35	0.48	$F = 1.11 \times 10^{-5} \times Ee$
FL04	NS Atlantic cod	1 093	0.52	0.71	$F = 3.25 \times 10^{-5} \times Ee$
	NS European plaice	1 894	0.21	0.57	$F = 1.11 \times 10^{-6} \times Ee$
	NS common sole	1 179	0.37	0.53	$F = 1.34 \times 10^{-5} \times Ee$
FL05	NS Atlantic cod	184	0.21	0.27	$F = 3.15 \times 10^{-5} \times Ee$
	NS European plaice	316	0.44	0.62	$F = 1.21 \times 10^{-5} \times Ee$
FL06	NS Atlantic cod	1 521	0.29	0.34	$F = 2.06 \times 10^{-5} \times Ee$
	NS European plaice	1 907	0.43	0.57	$F = 1.31 \times 10^{-5} \times Ee$
FL07	NS Atlantic cod	1 141	0.11	0.15	$F = 1.31 \times 10^{-4} \times Ee$
	NS European plaice	1 656	0.57	0.65	$F = 1.05 \times 10^{-6} \times Ee$
FL08	NS Atlantic cod	2 008	0.13	0.20	$F = 1.29 \times 10^{-5} \times Ee$
	NS European plaice	2 014	0.52	0.49	$F = 4.86 \times 10^{-6} \times Ee$
FL09	NS Atlantic cod	45 718	0.33	0.29	$F = 1.51 \times 10^{-7} \times Ee$
	NS haddock	31 984	0.20	0.41	$F = 2.40 \times 10^{-7} \times Ee$
FL10	NS European plaice	8 234	0.65	0.81	$F = 3.34 \times 10^{-6} \times Ee$
	NS commonsole	4 402	0.27	0.48	$F = 7.40 \times 10^{-7} \times Ee$
FL11	NS–WS saithe	854	0.64	0.62	$F = 1.69 \times 10^{-3} \times Ee$
FL12	CS Atlantic cod	2 102	0.27	0.29	$F = 2.06 \times 10^{-6} \times Ee$
	CS whiting	2 241	0.21	0.38	$F = 5.02 \times 10^{-5} \times Ee$
	CS–BB anglerfish	2 711	0.23	0.27	$F = 4.37 \times 10^{-6} \times Ee$
	NS–WS anglerfish	2 096	0.36	0.44	$F = 6.13 \times 10^{-5} \times Ee$
	NS–WS saithe	1 731	0.26	0.23	$F = 1.55 \times 10^{-8} \times Ee$
FL13	NS European plaice	3 111	0.73	0.75	$F = 3.55 \times 10^{-5} \times Ee$
	NS common sole	3 500	0.70	0.73	$F = 7.01 \times 10^{-5} \times Ee$
FL14	NS European plaice	46 270	0.73	0.74	$F = 2.55 \times 10^{-5} \times Ee$
	NS common sole	52 179	0.70	0.73	$F = 5.38 \times 10^{-5} \times Ee$
FL15	Northern European hake	2 646	0.34	0.60	$F = 1.43 \times 10^{-8} \times Ee$
FL16	Northern European hake	3 237	0.37	0.67	$F = 2.45 \times 10^{-7} \times Ee$
FL17	Northern European hake	2 685	0.60	0.66	$F = 2.31 \times 10^{-7} \times Ee$
	BB–CS anglerfish	1 778	0.46	0.46	$F = 4.05 \times 10^{-9} \times Ee$

Note: BB, Bay of Biscay; CS, Celtic Sea; NS, North Sea; WS, Western Scotland. Species investigated are anglerfish (*Lophius* spp.), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), European hake (*Merluccius merluccius*), European plaice (*Pleuronectes platessa*), saithe (pollock, *Pollachius virens*), common sole (*Solea solea*), and whiting (*Merlangius merlangus*).

cial exploitation of which has developed only since the early 1990s, so new aggregations are still being discovered. YE_SW may be an appropriate indicator to distinguish between area- and movement-specialists. However, it was not possible in this study to determine the factors that made an exploratory strategy more or less attractive than a stationary strategy. Such an investigation would require getting more insights in the factors that condition the fishers' decision-making process (e.g., spatial and time distribution of the harvested species, market shifts, management regulations).

Consider the other indices of fishing tactics and strategies (FT_DIST, FT_PATCH, YE_DIST, YE_PATCH, YE_IAC, YE_SW_METIER). The positive correlation between FT_DIST and FT_SW (also between YE_DIST and YE_SW) was expected, since the distance covered by a vessel during a fishing trip (or a year) is likely to increase with the number of rectangles visited. The negative correlation between FT_PATCH and FT_SW (also between YE_PATCH and YE_SW) could be explained by the fact that vessels fishing on aggregations are expected to visit less spatial units than vessels having a more scattered distribution. Overall, the impact of the other indices of fishing tactics and strategies on catch rates was limited. Regarding FT_DIST, FT_PATCH, YE_DIST, and YE_PATCH, a possible explanation is that

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Table 6. Output comparison of (*a*) the regression between log fishing mortality (log *F*) and log nominal fishing effort and (*b*) the regression between log *F* and log adjusted fishing effort (log Ee).

Fleet	Stock	*N*	R^2 (*a*)	R^2 (*b*)	Standard error of slope (*b*)	Equation (*b*)
FL01	NS Atlantic cod	1 970	0.13	0.59	0.02	log *F* = –10.01 + 1.00 × log Ee
	NS European plaice	2 200	0.05	0.53	0.02	log *F* = –12.05 + 0.96 × log Ee
	NS common sole	1 279	0.03	0.34	0.04*	log *F* = –9.31 + 0.90 × log Ee
FL02	NS Atlantic cod	3 003	0.13	0.53	0.02*	log *F* = –10.03 + 0.95 × log Ee
	NS European plaice	2 495	0.11	0.41	0.02	log *F* = –12.25 + 0.99 × log Ee
	NS common sole	1 216	0.14	0.47	0.03	log *F* = –10.86 + 0.97 × log Ee
FL03	NS Atlantic cod	1 089	0.08	0.45	0.03*	log *F* = –10.00 + 0.83 × log Ee
	NS European plaice	3 346	0.14	0.53	0.02*	log *F* = –12.13 + 0.93 × log Ee
	NS common sole	1 972	0.10	0.48	0.02*	log *F* = –11.19 + 0.83 × log Ee
FL04	NS Atlantic cod	1 093	0.05	0.37	0.04	log *F* = –10.49 + 0.95 × log Ee
	NS European plaice	1 894	0.17	0.67	0.02	log *F* = –13.76 + 0.98 × log Ee
	NS common sole	1 179	0.08	0.49	0.03*	log *F* = –11.10 + 0.88 × log Ee
FL05	NS Atlantic cod	184	0.07	0.06	0.13*	log *F* = –10.37 + 0.46 × log Ee
	NS European plaice	316	0.30	0.44	0.09*	log *F* = –12.99 + 1.44 × log Ee
FL06	NS Atlantic cod	1 521	0.03	0.04	0.05*	log *F* = –10.06 + 0.35 × log Ee
	NS European plaice	1 907	0.31	0.39	0.04*	log *F* = –12.99 + 1.42 × log Ee
FL07	NS Atlantic cod	1 141	0.03	0.11	0.05*	log *F* = –9.83 + 0.61 × log Ee
	NS European plaice	1 656	0.23	0.36	0.03*	log *F* = –14.36 + 1.08 × log Ee
FL08	NS Atlantic cod	2 008	0.02	0.10	0.04*	log *F* = –11.17 + 0.59 × log Ee
	NS European plaice	2 014	0.34	0.49	0.02	log *F* = –12.13 + 1.02 × log Ee
FL09	NS Atlantic cod	45 718	0.31	0.58	0.00*	log *F* = –14.79 + 0.99 × log Ee
	NS haddock	31 984	0.30	0.48	0.01*	log *F* = –15.02 + 1.02 × log Ee
FL10	NS European plaice	8 234	0.16	0.30	0.01*	log *F* = –12.01 + 0.77 × log Ee
	NS common sole	4 402	0.03	0.36	0.02*	log *F* = –13.97 + 0.88 × log Ee
FL11	NS–WS saithe	854	0.28	0.69	0.02*	log *F* = –6.34 + 0.95 × log Ee
FL12	CS Atlantic cod	2 102	0.17	0.23	0.02*	log *F* = –11.50 + 0.54 × log Ee
	CS whiting	2 241	0.07	0.23	0.02*	log *F* = –10.36 + 0.61 × log Ee
	CS–BB anglerfish	2 711	0.12	0.15	0.02*	log *F* = –12.74 + 0.48 × log Ee
	NS–WS anglerfish	2 096	0.04	0.16	0.05	log *F* = –10.38 + 0.99 × log Ee
	NS–WS saithe	1 731	0.00	0.05	0.05*	log *F* = –14.81 + 0.46 × log Ee
FL13	NS European plaice	3 111	0.26	0.29	0.03	log *F* = –10.45 + 1.01 × log Ee
	NS common sole	3 500	0.12	0.24	0.03	log *F* = –9.71 + 0.95 × log Ee
FL14	NS European plaice	46 270	0.32	0.34	0.01*	log *F* = –10.87 + 1.07 × log Ee
	NS common sole	52 179	0.16	0.30	0.01	log *F* = –10.00 + 1.01 × log Ee
FL15	Northern European hake	2 646	0.05	0.66	0.01*	log *F* = –18.04 + 0.96 × log Ee
FL16	Northern European hake	3 237	0.10	0.52	0.02*	log *F* = –15.24 + 0.94 × log Ee
FL17	Northern European hake	2 685	0.09	0.20	0.03	log *F* = –14.07 + 0.72 × log Ee
	BB–CS anglerfish	1 778	0.25	0.38	0.02*	log *F* = –17.32 + 0.69 × log Ee

Note: The standard error (SE) of the slope of regression (*b*) is indicated and marked with an asterisk (*) when the slope is significantly different from 1 ($p < 0.05$). BB, Bay of Biscay; CS, Celtic Sea; NS, North Sea; WS, Western Scotland. Species investigated are anglerfish (*Lophius* spp.), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), European hake (*Merluccius merluccius*), European plaice (*Pleuronectes platessa*), saithe (pollock, *Pollachius virens*), common sole (*Solea solea*), and whiting (*Merlangius merlangus*).

the validity of these indices is highly dependent on the spatial resolution used to define the basic observation cells. In this study, the basic spatial unit was the ICES statistical rectangle (1° longitude × 0.5° latitude). One ICES rectangle may host different species aggregations, especially when those are located at distinct depth strata (e.g., saithe and roundnose grenadier off Western Scotland). Given that fishing vessels search these aggregations, FT_DIST, FT_PATCH, YE_DIST, and YE_PATCH should really be calculated at a much finer spatial scale. Ideally, these indices should be derived based on haul-by-haul data, and the geographical position of fishing vessels should be accurately documented. Such data are currently being collected and analyzed by the participants of this exercise, and results of the analyses should be released in the near future. When such data become available, indices such as FT_DIST, FT_PATCH, YE_DIST, and YE_PATCH, but also alternative measures of the *E* dispersion (e.g., coefficient of variation, Clark and Evans coefficient of dispersion), could be examined in relation to catch rate variations.

The linkage between catch rates and métier choices generally highlights contrasts in fish availability and management regimes in the different areas fished, which may be illustrated by several examples. First, the North Sea Atlantic cod

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Fig. 10. Relationships between log-transformed partial fishing mortality (log *F*) and nominal fishing effort (log En) (*a*, *c*, *d*, *g*) and between log *F* and adjusted fishing effort (log Ee) (*b*, *d*, *f*, *h*). Data shown are for fleets FL04 harvesting North Sea European plaice (*Pleuronectes platessa*) (*a*, *b*) and common sole (*Solea solea*) (*c*, *d*) and FL08 harvesting North Sea European plaice (*Pleuronectes platessa*) (*e*, *f*) and common sole (*Solea solea*) (*g*, *h*).

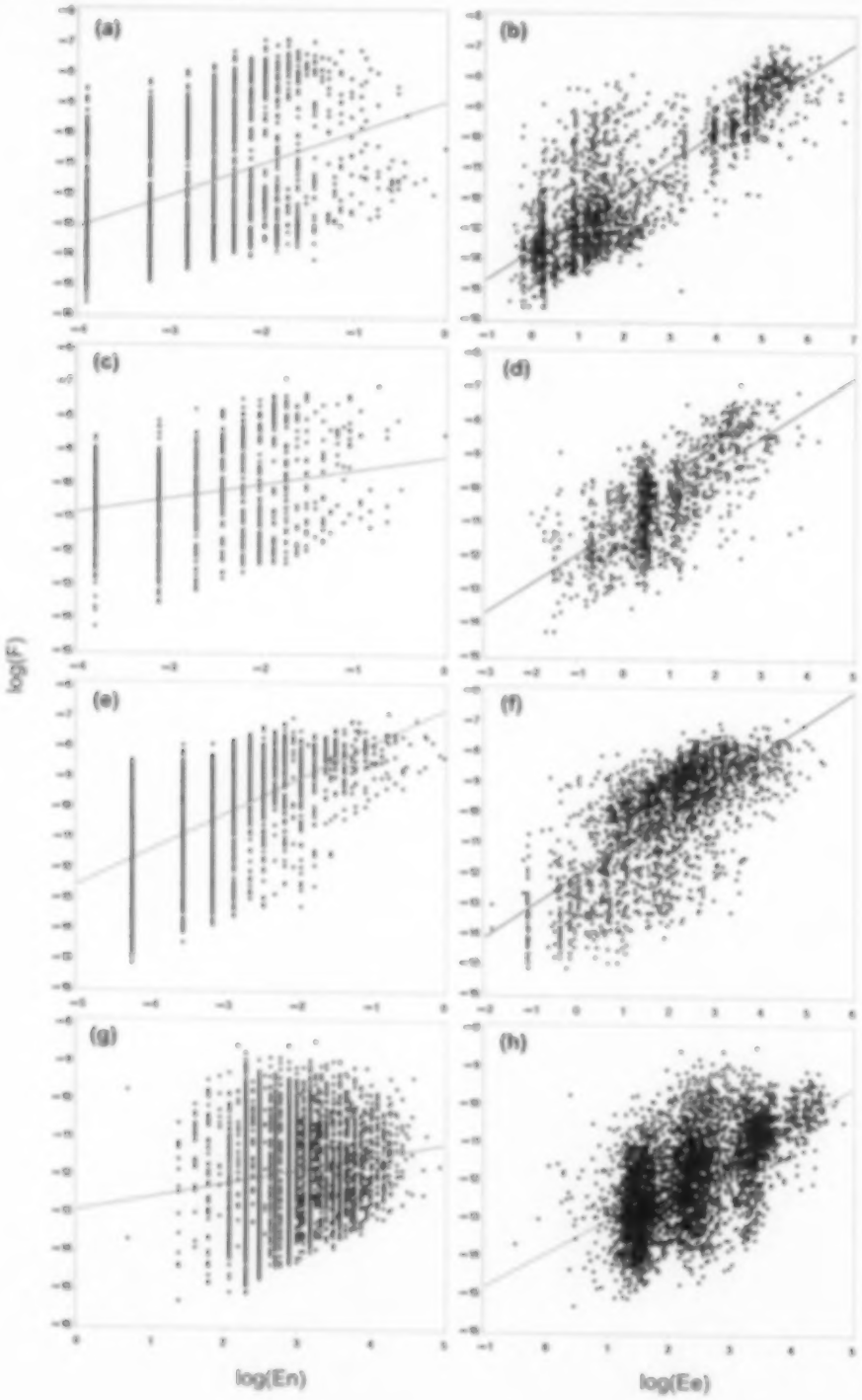

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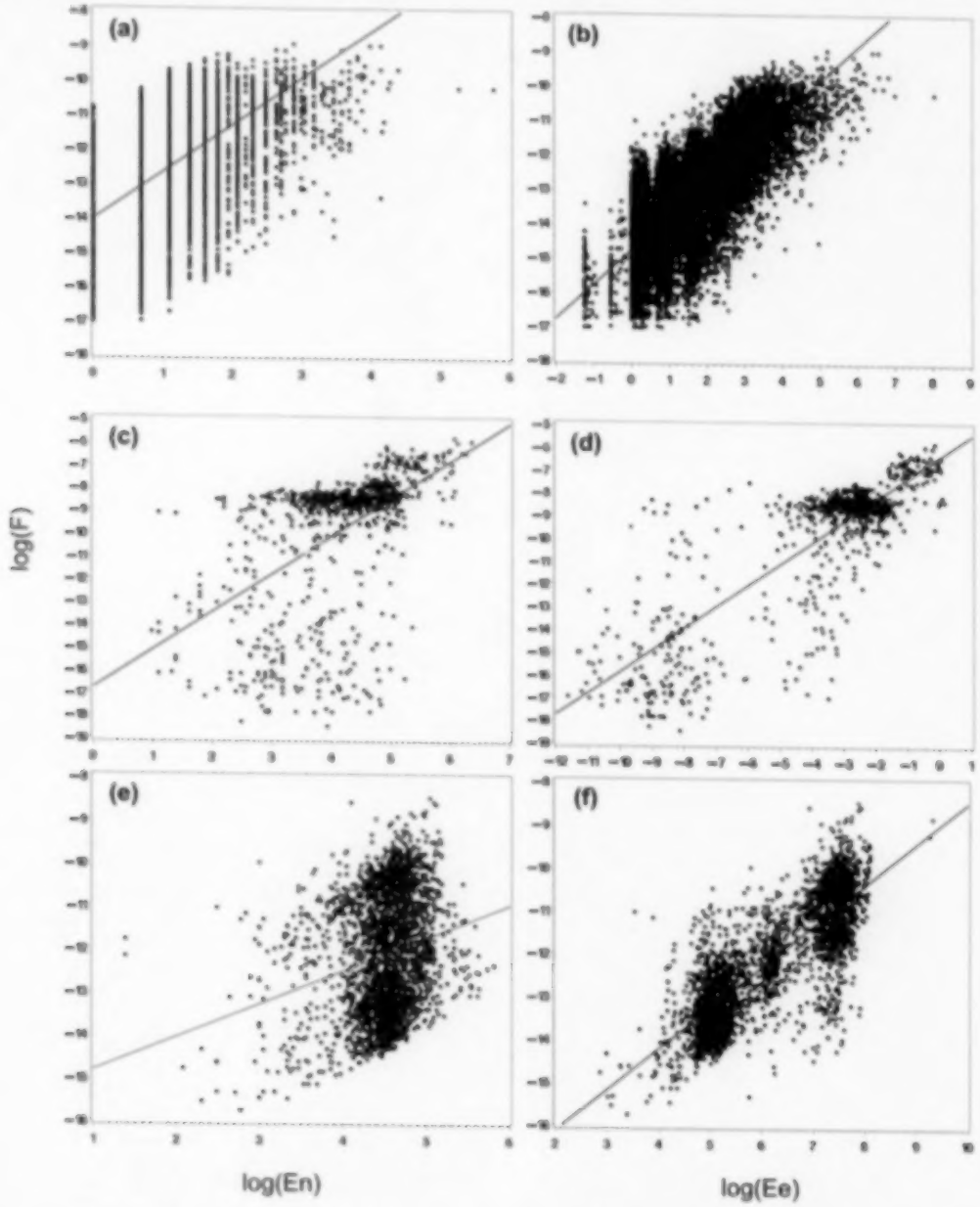
Fig. 11. Relationships between log-transformed partial fishing mortality (log F) and nominal fishing effort (log En) (*a*, *c*, *d*, *g*) and between log F and adjusted fishing effort (log Ee) (*b*, *d*, *f*, *h*). Data shown are for fleets FL09 harvesting North Sea Atlantic cod (*Gadus morhua*) (*a*, *b*), FL11 harvesting North Sea and Western Scotland saithe (pollock, *Pollachius virens*) (*c*, *d*), and FL15 harvesting northern European hake (*Merluccius merluccius*) (*e*, *f*).



stock has recently reached historical minima, and fishermen targeting this stock have to abide by restrictive management measures (e.g., low catch quotas, fishing effort limits). Management of Atlantic cod fishing is also restrictive in the Baltic Sea, but cod is by far the main demersal stock that is economically exploitable by fishers in that area. As a result, European plaice appears to be the main target species of fleets FL05–FL08 (Danish seiners and otter trawlers) in the North Sea, while the main target species in the Western Baltic Sea is Atantic cod. Second, for the Dutch and English beam trawlers harvesting common sole and European plaice, the most appropriate mesh size for plaice and sole fishing is directly linked with the different combinations of mesh size regulations and by-catch limits applicable in the North Sea.

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Third, with respect to saithe fishing, the mesh size associated with the highest catch rates is 110 mm for FL11 and 100 mm for FL12. This difference in mesh size likely results from the inconsistency in the mesh size regulations in force in the main areas visited by the vessels targeting saithe. Vessels belonging to FL11 target saithe mainly in the North Sea, where the minimal mesh size is 110 mm since 2001. Vessels from FL12 target saithe mainly off Western Scotland, where they have to abide by a minimal mesh size of 100 mm.

The fishing effort of the fleets under investigation was adjusted based on the analysis of the variations in catch rates in relation to both the fishing métiers and the indices of fishing tactics and strategies. The link between F and E was then investigated for the 38 combinations of fleets and stocks. In most cases, adjusting E led to a substantial gain in the precision of the relationship between F and E. In particular, for 11 of the 38 combinations of fleets and stocks, F was reasonably correlated and directly proportional to E. This result has implications for stock assessments and fisheries management. In terms of stock assessment, those fleets could be appropriate tuning fleets to assess the stocks under consideration. In terms of management, a unit reduction of those fleets' adjusted effort would lead to a unit reduction of F for the stocks they harvest.

Nevertheless, for 27 of the 38 combinations, F was poorly correlated and (or) not directly proportional to adjusted E. This indicates that this study takes one step in the right direction, but also that more research is needed to carry on the development of a reliable E model.

First, this study investigated the impact of tactical and strategic adaptations on catchability. Other aspects, including the technological development of fishing vessels, gears, and equipment on board, as well as time and spatial changes in fish availability, have not been investigated here. The influence of these factors on catchability has been evidenced in the past and sometimes used to adjust E (Kimura 1981; Fernö and Olsen 1994; Salthaug 2001). When the relevant data become available, an effort model could be developed that would combine both tactical changes and technological development.

Second, the results of this study are dependent on the quality of the catch and effort data derived from logbooks. In particular, misreporting and discarding are believed to occur in European fisheries, and such practices are likely to adversely alter data quality. Nevertheless, the data sets used for this exercise are also exploited to run routine ICES stock assessments under the auspices of the ICES, and they are currently believed to be the best source of data available to carry out fisheries analyses. An improvement would be to apply the methodology presented here to a data set where catch and effort data are accurately recorded on a haul-by-haul basis.

Third, catch rates in this study were analyzed for each fishing vessel independently, thereby ignoring the influence of vessel interactions (collaboration or competition) on catch rates. These aspects have been investigated by Gillis et al. (1993), Gillis and Peterman (1998), and Rijnsdorp et al. (2000*b*). For instance, Rijnsdorp et al. (2000*b*) showed that for the Dutch beam trawlers harvesting flatfish, a possible 10% increase in vessels revenue might be brought about when vessel density is reduced by 25%.

Fourth, improving the relationship between E and F requires not only to seek the most appropriate adjustment of E, but also to enhance the estimate of F. In this study, F was derived from ICES stock assessments and then partitioned into vessels and trips according to their relative catches. This simple approach, however, generates a number of concerns. The most obvious problem is that the relationship between F and E may not be evaluated when no reliable stock assessment outputs are available (e.g., blue ling, roundnose grenadier, black scabbardfish). Besides, when they exist, F estimates from stock assessments are uncertain, and more particularly so in the most recent years of the assessment, which correspond to the nonconverged part of the virtual population analysis. Finally, the fleets used in this study are sometimes also used as tuning fleets to calibrate the virtual population analysis (e.g., French trawlers for the North Sea saithe assessment), which may generate an undesirable case for circularity.

Finally, methods other than GLM could be contemplated to model catch rates. In particular, the delta-GLM could be helpful to model the catch rates characterized by a large proportion of zero values and highly skewed positive distributions (Dick 2004).

Further investigations could then be carried out to investigate the determinism of the shifts in fishing tactics and strategies. Fishermen's behavior highly depends on socio-economics, management regulations, and stock abundance (Holley and Marchal 2004). Modeling the linkage between shifts in management regimes and fishermen's behavior would complement approaches aiming at improving the relationship between F and E. The successful coupling of both compartments could directly benefit fisheries managers, who would be in a better position to forecast the responses of both fleets and fish stocks to shifts in management regimes.

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Integrating catch-at-age and multiyear tagging data: a combined Brownie and Petersen estimation approach in a fishery context

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Abstract: A comprehensive framework for modelling data from multiyear tagging experiments in a fishery context is presented that incorporates catch data into the traditional Brownie tag–recapture model. Incorporation of catch data not only allows for improved estimation of natural and fishing mortality rates, but also for direct estimation of population size at the time of tagging. These are the primary quantities required to be estimated in stock assessments — having an approach for directly estimating them that does not require catch rates provides a potentially powerful alternative for augmenting traditional stock assessment methods. Simulations are used to demonstrate the value of directly incorporating catch data in the model. Results from the range of scenarios considered suggest that in addition to providing a precise estimate of population size (coefficients of variation ranging from ~15% to 30%), including catch data can decrease biases in the mortality rate estimates (natural mortality especially) and improve precision of fishing mortality rate estimates (by as much as 60% at age 1). The model is applied to southern bluefin tuna (*Thunnus maccoyii*) tag–recapture and catch data collected in the 1990s to provide estimates of natural mortality, fishing mortality, and abundance for five cohorts of fish.

Résumé : Nous présentons un cadre exhaustif pour la modélisation de données provenant d'une expérience de marquage étalée sur plusieurs années et faite dans le contexte d'une pêche commerciale; il incorpore les données de capture au modèle traditionnel de marquage–recapture de Brownie. L'incorporation des données de capture permet non seulement une meilleure estimation des taux de mortalité naturelle et de mortalité due à la pêche, mais aussi une estimation directe de la taille de la population au moment du marquage. Il s'agit là de variables importantes qu'il est essentiel de déterminer dans les évaluations de stocks — le fait de posséder une méthode pour les déterminer directement sans utiliser les taux de capture fournit une puissante méthode de rechange pour enrichir l'arsenal de méthodes traditionnelles d'évaluation des stocks. Des simulations nous ont servi à démontrer l'avantage d'incorporer directement les données de capture dans le modèle. Les résultats obtenus dans la gamme des scénarios étudiés laissent croire qu'en plus de fournir une estimation précise de la taille de la population (coefficient de variation de ~15 à 30 %), l'inclusion des données de capture peut réduire les erreurs dans les estimations des taux de mortalité (de jusqu'à 60 % à l'âge 1). Nous appliquons le modèle à des données de marquage–recapture et des données de capture du thon rouge du sud (*Thunnus maccoyii*) récoltées dans les années 1990 dans le but d'obtenir des estimations de la mortalité naturelle, de la mortalité due à la pêche et de l'abondance chez cinq cohortes.

[Traduit par la Rédaction]

Introduction

Mark–recapture experiments represent one of the primary tools for studying the dynamics of wild animal populations, and an extensive literature exists documenting the wide variety of experimental designs and estimation models available (e.g., Seber 1982; Quinn and Deriso 1999; Morgan and Thomson 2002). The attraction of mark–recapture studies is that they have the potential to provide estimates of population abundance and mortality rates (both natural and exploitation). These are fundamental quantities needed for understanding population biology and providing scientific-based management advice, but are extremely difficult to measure directly for most wild populations because conduct-

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ing a direct census and (or) tracking a large number of individuals is often not feasible. There are two basic types of mark–recapture studies: those in which an animal can be captured and released multiple times and those in which only a single recapture is possible because the animal dies in the capture process. In most fishery applications, only single recapture studies are feasible, so only this type of study is considered here. Various names have been used to denote studies with single recaptures. We have chosen to refer to them as tag–recapture studies, as tags are usually used to mark fish.

In fisheries, natural mortality (M) and fishing mortality (F) rates are critical components of the stock assessment process because they form a key component in evaluating stock productivity and density-dependent responses of a population. Thus, uncertainty in their estimated values can be a major source of uncertainty in the resulting management advice. Direct estimation of F and M has generally been an intractable problem in marine fish populations. Most assessment methods assume that M is known and is constant with age and time, and values used come from ad hoc approaches (e.g., catch curve, life history characteristics, analogy from other stocks). Similarly, the most common approaches for estimating F (e.g., virtual population analysis and related catch-at-age approaches) are dependent upon assumptions about selectivity and require extensive, auxiliary, relative abundance indices.

Historically, the most common approaches for analysing tag–recapture data from a single release event were based on a Petersen-type model (e.g., Seber 1982). In this case, the primary quantity being estimated is the population size at the beginning of the experiment. Population size is estimated based on the ratio of the observed number of tags returned from samples taken from the population to the known number of tags released into the population. The Petersen method was developed for use in closed populations (i.e., populations that have no births, deaths, immigration, or emigration); however, the method can be applied to give an estimate of abundance at the time of tagging even when there are deaths and emigration, provided these factors apply equally to tagged and untagged animals. While the Petersen approach has been used extensively in wildlife and controlled experimental situations, it has not been widely used in large commercial fisheries because the size of the sample actually examined for tags is often difficult to ascertain and will almost certainly include error. In addition, if all recaptured tags are not reported, then Petersen models require that reporting rates are either known or estimable from other sources.

A different approach to the Petersen method is the use of multiyear tag release and recovery experiments (Brownie et al. 1985). Brownie models for multiyear tagging data provide estimates of total mortality rates from comparison of the return rates over time from the multiple releases. The power of the approach is that only data on the number of releases and returns (usually by cohort) are required to estimate mortality rates (i.e., there is no need to know the size of the sample examined for tags). Brownie models can provide estimates of total mortality rates even when reporting rates are unknown; however, the separation of M from F requires that reporting rates are either known or estimable. In theory, reporting rates can be estimated directly from multiyear tagging data if they are assumed to be constant over years, but the precision of the estimates is usually unsatisfactory (Hoenig et al. 1998*a*); moreover, reporting rates will vary by year in many situations. Thus, additional information is usually required for obtaining reasonable reporting rate estimates.

In recent years, the application of multiyear tagging experiments for estimating mortality rates using general models (Brownie et al. 1985) has been recognized as a powerful approach that can be applied in fishery situations to provide direct estimates of both M and F (e.g., Pollock et al. 1991; Polacheck et al. 1996; Frusher and Hoenig 2001). A number of studies have further developed these models for application in particular fishery situations (e.g., Hoenig et al. 1998*b*; Hearn et al. 1999; Pollock et al. 2002). In addition, estimates of mortality rates from multiyear tagging programs using a Brownie framework have been incorporated into stock assessments, and the approach underlies the design of a large-scale, international tagging program for southern bluefin tuna (*Thunnus maccoyii*; hereafter SBT) currently in progress (Anonymous 2001*a*, 2001*c*, 2002).

The Petersen and Brownie approaches rely on different information from tag–recapture data to estimate fundamentally different quantities (absolute abundance versus mortality rates). In particular, the Petersen method takes advantage of the information content in the proportion of recaptured animals that have a tag, while the Brownie approach uses the information content on the rate at which tags are returned. In this paper, we develop a tag–recapture model that combines these two approaches by using both sources of information to provide joint estimates of abundance and mortality rates. We do this in a fishery context in which catch data are used to provide estimates of the number of animals examined for tags, and the uncertainty in these catch statistics is incorporated explicitly. (The approach is equally valid in a more controlled experimental situation where exact information is available on the number of animals examined for tags.) We demonstrate that there is a synergy in combining the two approaches, in that the addition of catch data to the Brownie model not only allows for estimation of abundance but also improves estimation of mortality rates. Finally, we apply the combined model to SBT tag–recapture and catch data to provide estimates of M and F and abundance for five cohorts of fish from the early 1990s.

Methods

Basic dynamic model

The general population dynamics equations commonly used in fisheries form the basic model underlying the analysis of multiyear tagging experiments used here. These equations involve exponential and competing natural mortality (M) and fishing mortality (F) rates. The model can easily be translated into alternative formulations for the mortality dynamics, such as a net M and annual harvest rates from a pulse fishery (see Hoenig et al. 1998*a*). For a cohort of animals of a given age, the deterministic equations for the number of animals that survive to the next age and the number caught are as follows (e.g., Hilborn and Walters 1992, p. 378):

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Table 1. Expected number of returns at age from each release event in a multiyear tagging study involving a single cohort of fish.

		Expected no. of returns at age				
Release age	No. of releases	1	2	3	4	5
1	N_1	$N_1u_1\lambda_1$	$N_1S_1u_2\lambda_2$	$N_1S_1S_2u_3\lambda_3$	$N_1S_1S_2S_3u_4\lambda_4$	$N_1S_1S_2S_3S_4u_5\lambda_5$
2	N_2		$N_2u_2\lambda_2$	$N_2S_2u_3\lambda_3$	$N_2S_2S_3u_4\lambda_4$	$N_2S_2S_3S_4u_5\lambda_5$
3	N_3			$N_3u_3\lambda_3$	$N_3S_3u_4\lambda_4$	$N_3S_3S_4u_5\lambda_5$

Table 2. Expected number of fish caught at age from a cohort of fish with age-1 abundance of P_1.

	Expected catch at age				
Size of cohort	1	2	3	4	5
P_1	P_1u_1	$P_1S_1u_2$	$P_1S_1S_2u_3$	$P_1S_1S_2S_3u_4$	$P_1S_1S_2S_3S_4u_5$

$$(1)\qquad P_{i+1,t+1} = P_{i,t}\exp(-F_{i,t} - M_{i,t})$$

$$(2)\qquad C_{i,t} = \frac{F_{i,t}}{F_{i,t} + M_{i,t}} P_{i,t}[1 - \exp(-F_{i,t} - M_{i,t})]$$

where $P_{i,t}$ is the number of individuals of age i at time t; $C_{i,t}$ is the catch of individuals of age i at time t; $F_{i,t}$ is the instantaneous fishing mortality rate for individuals of age i at time t; and $M_{i,t}$ is the instantaneous natural mortality rate for individuals of age i at time t. In many contexts, $M_{i,t}$ is assumed to be constant with time, although multiyear and multicohort tagging programs can provide year- and age-specific M estimates (to a limited extent, as discussed later).

In the context of a tagging experiment, the above equations provide the basis for predicting the expected number of returns, assuming that the tagged fish constitute a representative sample of the population. In this study, we focus on a multiyear tagging experiment involving a single cohort of fish, so we can simplify the notation by dropping the t subscript and expressing everything in terms of age. The generalization of all equations to more than one cohort is straightforward. Later we will discuss some advantages of extending a tagging experiment to multiple cohorts, and we will also apply the integrated tag-and-catch model to multiple cohorts of SBT data.

Let N_a be the number of fish tagged at age a from a specific cohort and define

$$S_i = \exp(-F_i - M_i)$$

$$u_i = \frac{F_i}{F_i + M_i}(1 - S_i)$$

where S_i and u_i represent the annual survival and exploitation rates, respectively, of age i fish from the tagged cohort. Also, let λ_i be the reporting rate for tagged fish recaptured at age i ($0 \le \lambda_i \le 1$), because it is unlikely that all recovered tags will be reported, especially when recapture information comes from commercial fisheries. Then, following Brownie et al. (1985), expressions for the expected numbers of tags returned at subsequent ages from a cohort tagged at age a can be derived (Table 1). These expressions assume complete and instantaneous mixing of tagged fish with the untagged population and no tag-induced mortality or tag shedding. If these assumptions are not met, additional parameters and potentially additional data will need to be introduced to account for them. Failing to do so will likely lead to biased parameter estimates and an overly optimistic estimate of their precision (see Discussion).

Equations 1 and 2 can also be used to provide analogous expressions for the expected catches by age from a particular cohort, conditional on the size of the cohort at age 1, denoted by P_1 (Table 2). Conceptually, the catch data can be viewed as a tagging experiment in which the number of releases (P_1) is an unknown parameter to be estimated. However, unlike a tagging experiment where the numbers of returns by age from a particular release event are essentially known quantities, the numbers of fish caught by age will be estimated quantities, usually derived from a multistage sampling of catches for length combined with age–length keys derived from direct aging of hard parts (otoliths in the case of SBT). Because P_1 is unknown, it is not possible from the catch-at-age data alone to derive estimates of the mortality rates. Even if M is assumed known, it is still not possible unless F is also assumed to be constant for a cohort; this is the reason that catch-at-age stock assessment models require additional sources of data for "tuning" (see Hilborn and Walters 1992). Combining the catch-at-age data with the multiyear tagging data allows for P_1 to be estimated and for additional information on the F and M parameters contained in the catch data to be extracted.

Estimation model

We use a maximum likelihood approach to jointly model the tag–recapture and catch data. An independent likelihood term is developed for each data set, and these are multiplied together to give the overall likelihood function. A complexity is that the likelihood for the tag–recapture data involves reporting rates, which are not generally known and therefore must be estimated. Although tag–recapture data by themselves contain some information about reporting rates, the information is generally weak and insufficient to distinguish nonreporting from natural mortality and fishing mortality without making some fairly restrictive assumptions (see Hoenig et al. 1998*a*). Auxiliary data for estimating reporting rates can be obtained through a variety of methods. For some methods, such as tag seeding experiments, the data for estimating reporting rates can be considered independent of

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the tag–recapture and related catch data. In such cases, a likelihood term can be developed for the data and simply multiplied to the likelihoods for the tagging and catch data. For other methods, such as the use of observers on vessels, the reporting rate estimates use some of the tagging and (or) related catch data. In such cases, the likelihoods for the tagging and catch data need to be modified (we develop the likelihoods for a situation with observers in Polacheck et al. (2006)). For greatest generality, we assume here that the reporting rates have been estimated from an independent analysis (e.g., of tag seeding data) and that the estimates along with standard errors are available.

First consider the tag–recapture data. Recall that we are considering tagging data for a single cohort of fish tagged at multiple ages, where N_a is the number of fish from the cohort tagged at age a. If each fish of a given age has an equal probability of being recaptured (we consider the case where this is not true below), then the numbers of returns by age, plus the number not returned, from the releases at age a have a multinomial distribution. The likelihood function for the observed numbers of returns from the releases at all ages is the product of multinomials:

$$(3)\qquad L_{\mathbf{R}} = K\prod_a\left[\left(\prod_{i\geq a} p_{a,i}^{R_{a,i}}\right)(1-p_{a,\bullet})^{N_a-R_{a,\bullet}}\right]$$

$$K = \prod_a \frac{N_a!}{\prod_{i\geq a} R_{a,i}!(N_a-R_{a,\bullet})!}$$

where i indexes recapture age, $R_{a,i}$ is the number of tags returned from an age i fish released at age a, and $p_{a,i}$ is the probability of a tag being returned from an age i fish released at age a. An expression for $p_{a,i}$ can be obtained by dividing the expected number of returns in Table 1 by N_a. Explicitly,

$$p_{a,i} = \begin{cases} u_i\lambda_{i,} & i = a \\ S_a\cdots S_{i-1}u_i\lambda_{i,} & i > a \end{cases}$$

Note that in eq. 3 a dot in the subscript denotes summation over the index it replaces. Also, K is a constant that can be omitted when maximizing the likelihood.

Next consider the catch data. Similar to the tag–recapture data, if each fish of a given age from the cohort of interest (the one being tagged) has an equal probability of being caught, then the numbers of fish caught by age, plus the number not caught, have a multinomial distribution. However, the numbers of fish caught by age are not generally known precisely, but are estimated values. For many fisheries, the age distribution of the catch within a year is determined by taking a sample and using the age distribution of the sample to represent the age distribution of the total catch for the year. The error structure of the resulting catch-at-age estimates will depend on the sample size, the sampling procedure (e.g., simple random sampling or stratified random sampling), and the nature of the fishery (e.g., number of vessels and different gear types). In the simplest case where a random sample of n fish is taken from all fish caught in a year and the proportion of age a fish in the catch is π, the number of age a fish in the sample will have a binomial distribution with a coefficient of variation (CV) of $\sqrt{(1-\pi)/(n\pi)}$. In a more complex situation, such as when the catch is sampled from only a fraction of vessels and the age composition of the catch differs among vessels, then the distribution is not as clear and the sample size required to achieve this same CV would be larger (maybe substantially) than n. In addition, the ages of the fish in the sample are generally estimated, either from lengths and a growth curve or from direct aging of hard parts, and the total annual catch in numbers is often estimated from total weight. Both of these factors would result in increased variance in the catch-at-age estimates.

Table 3. Relative amount of the total variance in the catch-at-age data due to sampling error versus process error for different population sizes, levels of overdispersion (ϕ), and coefficients of variation (CV) in the catch sample.

ϕ	Population size	Sample CV	Relative variance
1	10 000	0.10	5.3
	100 000	0.10	52.6
	10 000	0.35	64.5
	100 000	0.35	644.7
3	10 000	0.10	1.8
	100 000	0.10	17.5
	10 000	0.35	21.5
	100 000	0.35	214.9

Note: $\phi = 1$ means no overdispersion (i.e., multinomial data). Catch probability was 0.05 for all scenarios.

The actual structure of the sampling error in a particular situation will depend on the details of the sampling and age estimation procedures. We have chosen to model it using a Gaussian distribution because this provides a general framework for exploring the effects of measurement error in the catch estimates. However, other error structures for the catch data that accommodate a particular sampling regime can easily be incorporated as long as an appropriate likelihood function can be developed. We have also assumed that the errors in the catch-at-age estimates between years (i.e., ages for a single cohort) are independent. This is a reasonable assumption for many fisheries, in which sampling and aging data are collected each year. However, in some situations (particularly where age at length is being estimated from a growth curve), covariance in the estimates between years may exist and should be accounted for.

To fit a model with both multinomial process error and Gaussian sampling error in the catch data would require additional complexity (e.g., using a Kalman filter) with no anticipated gain in estimation performance. This is because the relative size of the multinomial error compared with the sampling error is expected to be small in most commercial fishery situations. The relative size of the errors depends on the population size of the cohort being caught, the probabilities of capture, and the sample variance. When the population size is reasonably large (>10 000), as would be expected in most commercial fishery situations, the multinomial error is negligible compared with the Gaussian sampling error (Table 3). In such situations, only the sampling error needs to be included in the model because it will be the dominant

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source of catch error contributing to the variance of the parameter estimates.

Let C_i be the actual number of fish caught at age i and $\hat{C}_i = C_i + e_i$ be the estimated number of fish caught at age i, where e_i has a Gaussian distribution with mean 0 and variance σ_i^2. Because we are assuming that the process error in the catch is negligible compared with the sampling error, $\hat{C}_i$ is approximately Gaussian distributed with mean $E(C_i)$ (as given in Table 2) and variance σ_i^2. Thus, the likelihood for the catch-at-age data can be expressed as

$$(4) \qquad L_C = \prod_i \frac{1}{\sqrt{2\pi\sigma_i^2}} \exp\left\{-\frac{1}{2\sigma_i^2}[\hat{C}_i - E(C_i)]^2\right\}$$

Lastly, consider the reporting rate data. The data we assume to be available are a reporting rate estimate for each year of recapture, $\hat{\lambda}_i$, and a standard error for the estimate, $\sigma_{\hat{\lambda}_i}$. We assume that $x_i = n_i\hat{\lambda}_i$ is the number of tags reported at age i, and x_i is binomial with probability λ_i and sample size n_i. Note n_i can be thought of as the sample size required to achieve the level of precision in the reporting rate estimate specified by $\sigma_{\hat{\lambda}_i}$ (e.g., it could be the required number of seeded tags). Using the variance formula for a binomial distribution, we know that $\mathrm{Var}(\hat{\lambda}_i) = \lambda_i(1-\lambda_i)/n_i$. We also know that $\mathrm{Var}(\hat{\lambda}_i) = \sigma_{\hat{\lambda}_i}^2$. Setting these equal, we can solve for the sample size as

$$n_i = \frac{\lambda_i(1-\lambda_i)}{\sigma_{\hat{\lambda}_i}^2} \approx \frac{\hat{\lambda}_i(1-\hat{\lambda}_i)}{\sigma_{\hat{\lambda}_i}^2}$$

Thus, the likelihood for the reporting rates can be specified as

$$(5) \qquad L_\lambda = \prod_i \frac{n_i!}{x_i!(n_i-x_i)!}\lambda_i^{x_i}(1-\lambda_i)^{n_i-x_i}$$

where $n_i = \hat{\lambda}_i(1-\hat{\lambda}_i)/\sigma_{\hat{\lambda}_i}^2$ and $x_i = n_i\hat{\lambda}_i$.

The overall likelihood can be obtained by multiplying the three likelihood components given in eqs. 3, 4, and 5 together:

$$(6) \qquad L = L_R L_C L_\lambda$$

It is legitimate to multiply likelihoods together provided they are independent of one another. The assumption that the tag–recapture and catch data are independent may not be met if during the process of sampling the catch data, tags are found and returned; however, we assume that tags are removed at the time of catch, prior to catch sampling. Moreover, if the catch sample is relatively small (as would be expected in most commercial fishery situations), then the expected number of tags in the sample will be so small that the independence assumption will not be seriously violated.

Estimates of the unknown model parameters can be obtained by maximizing the likelihood in eq. 6 or, equivalently (and more standard in practice), by minimizing the negative log of the likelihood. However, not all parameters introduced thus far are estimable. First, the information for estimating M_i comes from the differential between the expected returns at age $i+1$ of fish released at age i and those released at age $i+1$. Thus, in an experiment with I consecutive release years, estimates can only be obtained for $I-1$ of the natural mortality rate parameters (regardless of the number of recapture years). We address this issue in our simulations by assuming that $M_i = M_{i-1}$ for $i \geq I$, but other constraints could be used, such as imposing a parametric relationship between M and age (which we illustrate when fitting the model to SBT data).

Second, the catch variance parameters are not directly estimable. In our simulations, we assume the σ_is are known. In practice, estimates of the catch-at-age are generally derived from a sampling program, and therefore independent information should be available for estimating the σ_i parameters. These estimates could be treated as known or, more rigorously, included in the model through an additional likelihood component. It is also possible in theory to deal with this issue by putting constraints on the variance parameters. However, it transpires that even if the σ_is are constrained to be equal at all ages (i.e., $\sigma_i = \sigma$ for all i), σ is generally still not estimable. This is because, by allowing a separate F for each age of recapture, the catch likelihood (eq. 4) can always be maximized by allowing σ to approach zero. Specifically, F_i values can be found that give a perfect fit to the catch-at-age data (i.e., such that $E(C_i) = C_i$ for all i), in which case the exponential term in the catch likelihood equals one (provided $\sigma > 0$) and the catch likelihood approaches infinity as σ approaches zero. Even if the F_i values that perfectly fit the catch data do not fit the recapture data well, the catch component of the likelihood will still dominate over the tag–recapture likelihood when σ is sufficiently close to zero. In situations where the tagging data are relatively influential compared with the catch data (such as when the number of tag releases is large, the error in the reporting rates is small, and the variability in the catch data is large), there will often be a local maximum away from zero (we see an example of this when we fit the model to SBT data). In such situations, a reasonable estimate of σ can be obtained by setting a lower bound on σ sufficiently larger than zero. Generating a likelihood profile for σ is a good way to determine when a local maximum exists. Note, however, that simulations suggest that even when a local maximum exists, the local estimate of σ tends to have a negative bias.

Overdispersion in the tag–recapture and catch data

The estimation model assumes a multinomial distribution for the tag–recapture data. This is only valid if all fish of a particular age have the same probability of being caught. If there is unsystematic, incomplete mixing (see Discussion) of tagged and untagged fish, such as when fish tagged in the same school and (or) in close proximity on the same day have positively correlated recapture probabilities, then the number of recaptures at age will have more variability than a multinomial distribution predicts. Differential age or size selectivities among fishing vessels will also contribute to overdispersion if tagged fish are not homogeneously mixed within the untagged population. One way of incorporating this overdispersion is to model the tag–recapture data as Dirichlet–multinomial. Essentially, the probabilities of return corresponding to releases at a given age are themselves modelled as random Dirichlet variables (Appendix A). Then the numbers of returns by age conditional on the probabilities of return follow a multinomial distribution, and the unconditional numbers of returns by age follow the compound distri-

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bution referred to as the Dirichlet–multinomial (Appendix A).

It is possible to replace the multinomial tag–recapture likelihood with a Dirichlet–multinomial likelihood and to parameterize the model such that the amount of variance in the recapture data is ϕ times that of multinomial recaptures (Appendix A). However, we found in simulations that ϕ is not estimated reliably; in fact, it almost always converges to a lower bound of one. This is a common problem in the estimation of overdispersion parameters. A number of approaches can be used to deal with the problem. First, a value for the overdispersion parameter can be inputted into the model either as known or with error (say, through another likelihood term); however, it seems unlikely that a reasonable value would be known or could be estimated independently of the tag–recapture data. Second, modified estimation methods could be used. For example, restricted maximum likelihood is often used for fitting models with variance parameters that are inestimable using standard maximum likelihood and may have potential here, but would require developing procedures specific to this situation. Alternatively, Kitada et al. (1994) proposed using a Gaussian approximation to the Dirichlet–multinomial; however, the statistical properties of the resulting parameter estimates need investigating. Third, the multinomial likelihood can be used for the recapture data — the parameter estimates should still be unbiased but their estimated standard errors obtained from traditional likelihood methods (i.e., from the inverse Hessian matrix) will be too small. Bootstrapping is one method of obtaining more realistic standard error estimates. For example, if the overdispersion stems from a high degree of school fidelity, then the data could be resampled using schools as the basic sampling unit. Another possibility is to post-estimate the amount of overdispersion and inflate the standard error estimates accordingly. Such an approach is described in McCullagh and Nelder (1989, pp. 174–175); however, they are dealing with a simpler model, and the simulation results presented below suggest that a more sophisticated approach may be required for our model.

If overdispersion exists in the recapture data, then it may also exist in the catch data. As discussed previously, the sampling error in the catch-at-age data will generally dominate the multinomial process error so that the process error can be ignored. Whether this is the case when the catch-at-age data are overdispersed multinomial will now depend not only on the population size, the capture probabilities, and the level of sampling error, but also on the level of overdispersion. Even so, the sampling error still dominates in most situations (Table 3). Only when the population size is 10 000 or fewer, the CV in the catch sample is 0.10 or more, and ϕ is 3 or more does it appear that the process error would need to be accounted for.

Simulation methods

To examine the behaviour of the integrated model and, in particular, to investigate the effect of incorporating catch-at-age data on the accuracy and precision of the parameter estimates, we conducted a series of Monte Carlo simulations. We considered a tagging experiment in which a single cohort of fish is tagged in 3 consecutive years starting at age 1 (i.e., at age 1 in year 1, age 2 in year 2, and age 3 in year 3) and recaptured over the same 3 years. Catch data are also assumed to be available for the cohort over these 3 years. We generated recapture data corresponding to the releases at each age using a Dirichlet–multinomial distribution with given values for the number of releases (N_a), the fishing and natural mortality rates (F_i and M_i), the reporting rates (λ_i), and the overdispersion factor (ϕ). We generated catch data first using a Dirichlet–multinomial distribution with a given value of P_1 and the same F, M, and ϕ values used for the recapture data and then adding additional Gaussian sampling error with a constant CV, which we will denote by υ, at all ages. In both the recapture and catch data, we used a Dirichlet–multinomial distribution instead of a multinomial distribution because overdispersion is likely to exist in most fishery situations and we did not want to provide overly optimistic or unrealistic expectations about what might be achieved with tagging experiments of this type. An estimate of the reporting rate in each year of recapture ($\hat{\lambda}_i$) was generated using a beta distribution with mean equal to the true reporting rate λ_i and standard deviation of σ_{λ_i}. The actual parameter values used for all data sets depended on the scenario being considered.

To estimate the parameters, we used the estimation model with a multinomial likelihood for the recapture data and a Gaussian likelihood for the catch data. By doing so, we were able to see whether this simplified but pragmatic estimation model provided adequate performance. In particular, we could compare the variances of the parameter estimates from multiple realizations of the Monte Carlo simulations with the variance estimates from the inverse Hessian matrix to see how much the latter were underestimated by not accounting for the overdispersion.

For each scenario considered, we simulated 500 sets of tag–recapture data with corresponding reporting rate and catch-at-age data. For each set of simulated data, we estimated the parameters first using the model with just tag–recapture and reporting rate data (leaving out the catch component of the overall likelihood) and second using the model including catch data. We calculated the improvement in the precision of the parameter estimates due to including catch data as the standard deviation (SD) of the estimates from the model with catch data divided by the SD of the estimates from the model without catch data. (Note that this cannot be calculated for P_1 because the model without catch data does not provide an estimate of the initial population size.)

For simplicity, we always generated the data using constant values across ages for M, F, and λ, but the model estimated a separate F for each age (F_1, F_2, and F_3), a separate λ for each age (λ_1, λ_2, and λ_3), and a separate M for age 1 (M_1) and ages 2 and above (M_2) — recall this is the most we can estimate with 3 release years. The model also provides a direct estimate of the initial size of the cohort, P_1, when the catch data are included.

Results

Simulation results

We first considered a scenario with tag releases of N_a = 250 for a = 1,...,3; mortality rates of F_i = 0.15 and M_i = 0.20 for i = 1,...,3; reporting rates of λ_i = 0.70 for i = 1,...,3; and an age 1 population size of P_1 = 100 000. We set

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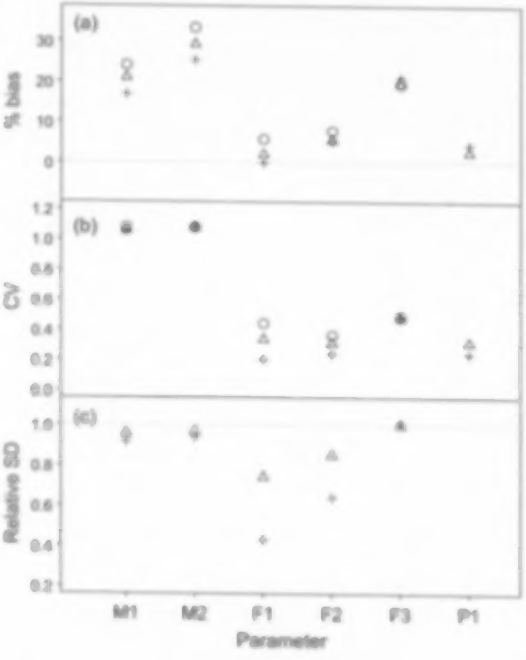
the level of overdispersion in the recaptures and catches to be $\phi = 3$ (i.e., variance three times larger than multinomial data), the SD for the reporting rate estimates to be $\sigma_{\lambda_i} = 0.10$ for $i = 1,\ldots,3$, and the CV of the catch data to be $\upsilon = 0.10$ for all ages (corresponding to a simple random sample of size 900 in each year when the proportion of age i fish in the total catch for year i is 0.10).

The bias and CV of the parameter estimates from the 500 runs are compared for the model with and without catch data (Fig. 1). Also shown is the improvement in the precision of the parameter estimates from including catch data (as defined in the Simulation methods section). Including catch data improved the precision of the F estimates at ages 1 and 2 substantially, with a 57% reduction in the SD of the F_1 estimates and a 36% reduction in the SD of the F_2 estimates. The precision of the M estimates also improved, although to a much lesser extent (8% reduction in SD for M_1; 6% reduction in SD for M_2). While some improvement in precision is to be expected because the catch data constitute additional data, it is substantial for some parameters, particularly in light of the fact that catch-at-age data are often available without any additional expense. Improvements would be expected with more tagging data as well but would come at an additional, often considerable, cost. Integrating catch data into the model also provides a direct estimate of P_1, which cannot be obtained from the tag–recapture data alone. In our simulations, P_1 was estimated reasonably precisely, with a CV of about 25%. Note that the model estimates of the reporting rates are not shown because they are not of primary interest and, moreover, they are always estimated without bias and with precision essentially equal to the precision of the inputted estimates.

The results will clearly depend on the specifics of the situation, with the most influential factor being the precision of the catch data. In this first scenario, we have assumed relatively precise catch data (CV of 0.10 for all ages). Thus, we considered a second scenario in which we set the CV of the catch data to be 0.35 for all ages (corresponding to a simple random sample of size 75 in each year when the proportion of age i fish in year i is 0.10, but likely to a much larger sample size in actuality — see prior discussions). As expected, the benefits of including catch data were reduced; however, improvements in precision were still substantial for some parameters (Fig. 1). In particular, there was still a 25% reduction in the SD of the F_1 estimates and a 15% reduction in the SD of the F_2 estimates.

Large biases were apparent in some of the mortality rate estimates (Fig. 1). Including catch data decreased the bias in both M_1 and M_2 by about 8% when the catch CV was 0.10 and by about 3%–4% when the catch CV was 0.35. It also reduced the bias in F_1 noticeably. Nevertheless, the biases were still substantial for M_1, M_2, and F_3 and appeared to increase exponentially with age for the F estimates (this pattern was confirmed using simulations with additional recapture years). Increasing the number of releases from 250 to 1000 at each age essentially eliminated the biases (Fig. 2). As expected, the CVs of all parameters also decreased, but more interestingly, the relative gain in precision from incorporating catch data remained almost as great as when the number of releases was 250.

Fig. 1. Comparison of parameter estimates obtained from 500 simulations, with 250 releases per year and $\phi = 3$, using the model without catch data (circles) versus the model with catch data (pluses for $\upsilon = 0.10$; triangles for $\upsilon = 0.35$). Shown are (*a*) percent bias; (*b*) coefficient of variation (CV); and (*c*) standard deviation (SD) from the model with catch data relative to the model without catch data. The horizontal line in (*a*) indicates zero bias; the line in (*c*) indicates no improvement in parameter precision by including catch data. υ, CV of catch data; ϕ, overdispersion factor; M_i, natural mortality rate for age i; F_i, fishing mortality rate for age i; P_1, age-1 cohort size.



The true parameter values will obviously have an effect on the results. For example, higher Fs would result in more tag returns and greater accuracy and precision in the estimates. We have explored the model over a range of mortality rate values, and our general conclusions regarding the value of incorporating catch data were not changed. Because the parameter expected to have the greatest impact on the results is ϕ, we present simulation results for when we varied this parameter. We have already considered a number of scenarios with $\phi = 3$ (i.e., 250 or 1000 releases; catch CV of 0.10 or 0.35). We ran these same scenarios using $\phi = 1$ (which gives multinomial data) and $\phi = 9$. Not surprisingly, we found that the absolute accuracy and precision of the parameter estimates were appreciably affected (obviously becoming poorer with increased overdispersion), but that the relative improvement in the precision of the parameter estimates from including catch data remained remarkably similar. For example, whether ϕ was 1, 3, or 9 and whether the number of releases at each age was 250 or 1000, the SD of the F_1 and F_2 estimates decreased by 40%–60% and 30%–

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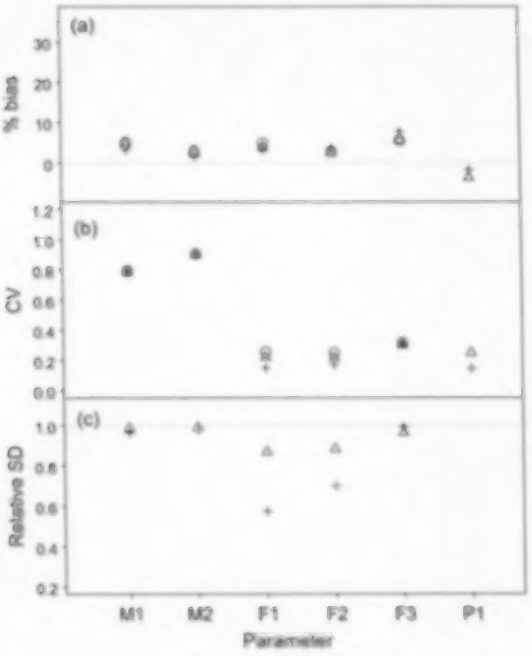
Fig. 2. Comparison of parameter estimates obtained from 500 simulations, with 1000 releases per year and $\phi = 3$, using the model without catch data (circles) versus the model with catch data (pluses for $\upsilon = 0.10$; triangles for $\upsilon = 0.35$). Shown are (*a*) percent bias; (*b*) coefficient of variation (CV); and (*c*) standard deviation (SD) from the model with catch data relative to the model without catch data. The horizontal line in (*a*) indicates zero bias; the line in (*c*) indicates no improvement in parameter precision by including catch data. υ, CV of catch data; ϕ, overdispersion factor; M_i, natural mortality rate for age i; F_i, fishing mortality rate for age i; P_1, age-1 cohort size.



40%, respectively, when the CV of the catch data was 0.10; these values decreased by 10%–25% and 10%–15%, respectively, when the CV of the catch data was 0.35.

Throughout our simulations, we have assumed that the CV of the catch data is known correctly. We investigated the effect of assuming the wrong catch CV and found that it was generally small, in terms of both the bias and precision of the parameter estimates. For example, in the scenario with 250 releases, ϕ of 3, and a true catch CV of 0.35, there were no appreciable effects of assuming the catch CV was 0.20 or 0.50 instead of 0.35 (the largest change in bias being 5% and generally less than 2%; the largest change in SD being 8% and generally less than 2%). Only when the catch CV was assumed to be as low as 0.05 or as high as 0.75 were any large effects seen. In particular, when the CV was 0.05, the SDs of the F estimates were overestimated by 20%–55%, but biases of all parameters were still on the order of 5%–10%. When the CV was 0.75, the P_1 estimate showed a negative bias of about 15% and its SD was underestimated by about 13% (the effect on other parameters was less). These results suggest that the consequences of assuming the wrong catch CV will generally not be serious.

Lastly, for each scenario we compared the SDs of the parameter estimates obtained from the 500 simulation runs (which approximate the true standard errors of the estimates) with the standard error estimates obtained from the inverse Hessian matrix (these are obtained for every run, so we averaged over the 500 runs). For the scenarios with multinomial data ($\phi = 1$), the estimates were very similar for the two methods, as we had hoped. For the scenarios with $\phi = 3$ and $\phi = 9$, the Hessian-based standard error estimates for the Ms were underestimated by a factor of about $\sqrt{\phi}$. However, for the Fs and P_1, the factor by which the Hessian-based standard error estimates were underestimated was not as predictable. It was generally in the range of 60%–90% of $\sqrt{\phi}$ and tended to be slightly smaller for P_1 than for F and also to be slightly smaller at the higher level of overdispersion.

Application to SBT

SBT are a long-lived, pelagic species found throughout much of the southern oceans. Adults of about 10 years and older spawn in the northeast Indian Ocean between Indonesia and the northwest coast of Australia, generally between the months of September and April. Juveniles (ages 1 to 4) tend to spend their austral summers in southern coastal waters, with ages 0 to 2 commonly found south of Western Australia (WA) and ages 1 to 4 commonly found off South Australia in the Great Australian Bight (GAB). During the winter, juveniles tend to be found in deep oceanic waters, particularly after age 1. The proportion of the global stock of each age class found off WA and in the GAB during the summer months is not known; however, it is thought to be relatively high but diminishing with age. SBT are harvested by a number of different fishing fleets and countries. In particular, juveniles are harvested primarily by Australian purse seiners operating within the GAB during the summer and to a lesser extent by various Japanese, Korean, and Taiwanese longline fleets operating on the high seas (i.e., the Tasman Sea, southeast Indian Ocean, and waters off South Africa) mainly during the winter.

Extensive tagging operations were carried out on SBT in the 1990s in which juvenile fish were caught, tagged, and released primarily in the coastal waters south of WA and in the GAB. All fish were double-tagged. The tag numbers and length of each fish were recorded, together with the location and date of release. Multiple age classes, generally ages 1 to 3, were tagged in each year. A fish's age at tagging was estimated based on its length using the method currently adopted by the Commission for the Conservation of Southern Bluefin Tuna for its stock assessments (Anonymous 2001*b*). SBT grow rapidly as juveniles, so there is good separation between length distributions of the ages being tagged, and therefore the number of aging errors should be small. All tagging was done between November and April, so the ages were adjusted in order that fish caught in November or December from a given year class (cohort) were assigned the same age as those tagged after December. Recaptures occurred in the commercial fisheries throughout the geographical distribution of SBT, ranging in longitude from

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0° to 180°E and in latitude from 30° to 50°S. Upon recapture, the finder measured the caudal fork length of the fish and recorded this length as well as the tag number, the date and location of recapture, and sometimes the weight of the fish. This information, along with one or both of the tags, was sent to CSIRO (Commonwealth Scientific and Industrial Research Organisation, Marine and Atmospheric Research, Hobart, Tasmania, Australia). Recapture age was determined using the estimated release age and the time between release and recapture. (Further details regarding the tagging operations and the data compilation procedures are provided in Polacheck et al. (2006).)

SBT are caught by a number of different fishing fleets and countries and the catch information available for each component differs considerably; thus, compiling total catch numbers by age is a complex process. The catch-at-age data used in our analysis are taken from the catch-at-age data used in the 2004 stock assessments for SBT conducted by CSIRO. The only substantial difference is that the catch-at-age data for the assessments were compiled by calendar year, whereas for our analysis they were compiled by fishing year, defined as 1 November of the previous year to 31 October of the given year. This year definition is consistent with the age definition being used and is also more consistent with the timing of the major fisheries for SBT, especially the Australian purse seine fishery, which generally operates from November or December to April and catches the majority of juvenile SBT. It should be noted that for the tagging data, release year and recapture year also refer to fishing year, as opposed to usual calendar year. (More information about the fishery components and the processing and compiling of the catch data are provided in Polacheck et al. (2006).)

Estimating reporting rates for SBT is complicated because the fishery comprises multiple components with varying reporting rates and because the data are very limited. A relatively small amount of observer data and tag seeding data exist, and these data have been used along with a number of alternative assumptions to provide year- and age-specific estimates of reporting rates for SBT from 1991 to 1997 (Eveson and Polacheck 2005). That document presents a number of alternatives, but the reporting rate estimates used in our analysis correspond with those given in option 8 of their table 5*a*; this was chosen because it is the most highly information-based option. We set σ_{λ_i} to be 0.10 for all ages. In a more rigorous analysis for the purpose of evaluating the SBT stock, we would consider the effect of varying this value and also check the sensitivity of the results to the reporting rate alternative chosen. Moreover, because the reporting rate estimates involve some observer data (i.e., return rates of tags from vessels with observers versus vessels without observers), they are not completely independent of the tag–recapture and catch data (note that observer data were not used in estimating the catch-at-age). Nevertheless, we do not expect the violation to be serious, nor do we expect the results to be appreciably affected.

SBT release and recapture data, catch data, and reporting rate estimates for years 1991–1997 are used in our analysis (Table 4). Although recapture and catch information exist beyond 1997, reporting rate estimates are not available beyond this year so we cannot include additional years in our analysis. Furthermore, we only include recapture information (and corresponding catches) up to a maximum of age 5 because the number of tag returns beyond age 5 is relatively small and because the constraints put on natural mortality are less likely to hold true at older ages.

Tag–recapture data exist for multiple cohorts of SBT; therefore, we can apply the joint tagging and catch model to each cohort separately (using the model equations directly as they were presented), or we can apply the model to all cohorts simultaneously (by modifying the equations to have an additional subscript for year). These two options are equivalent if each cohort has a unique set of parameters (i.e., all parameters are allowed to differ between cohorts). However, for SBT (and for most species), M is assumed constant over time when conducting stock assessments. Thus, in our analysis, we still allow for natural mortality to differ between ages, but not between cohorts. To implement this restriction requires all cohorts to be modelled simultaneously.

We assume the catch-at-age data are Gaussian-distributed with a constant CV across ages and also years (since we have multiple cohorts). We expect the uncertainty in the catch-at-age data for SBT to be fairly large because of errors in the age distribution (from sampling variability and errors in the age estimates) and because of errors in the total catch numbers (from under-reporting as well as from difficulties in compiling catch data in a fishery comprising multiple nations and fleets). In the results presented, we assumed a CV of 0.30.

In applying the model to SBT data, we modified the tag–recapture component to allow for F to differ between tagged fish in the year of tagging and untagged fish in that same year (following the model presented in Hoenig et al. 1998*b*). This is to allow for the fact that newly tagged fish would not be fully mixed with the untagged population immediately after tagging; also, tagging generally occurs during the fishing season, so tagged fish are only vulnerable for part of the season. We assume that tagged and untagged fish are fully mixed by the year following release (recall all tagging of SBT occurred between November and April, so this allows several months for mixing to occur). The modified return probabilities are given by

$$p_{a,i} = \begin{cases} u_i^* \lambda_r & i = a \\ S_a^* u_i \lambda_r & i = a+1 \\ S_a^* S_{a+1} \cdots S_{i-1} u_i \lambda_r & i > a+1 \end{cases}$$

where $S_i^* = \exp(-F_i^* - M_i)$, $u_i^* = [F_i^*/(F_i^* + M_i)](1 - S_i^*)$, and F_i^* is the instantaneous fishing mortality rate for age i fish tagged at age i. All other parameters are defined as before. Here, S_i^* and u_i^* represent the annual survival and exploitation rates, respectively, of fish in the year that they are tagged, whereas S_i and u_i represent the annual survival and exploitation rates, respectively, of fish in the years following tagging. Note that the model proposed by Hoenig et al. (1998*b*) cannot provide an estimate of F_1, only F_1^*, but by incorporating catch data, both parameters can be estimated.

We also constrained M to be a linear function of age rather than the same at ages 2 and above. This constraint is more consistent with the M values generally assumed in stock assessments for SBT, which decline with age. We parameterized the linear function in terms of M at the youn-

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Table 4. Southern bluefin tuna (*Thunnus maccoyii*) data used in the analysis.

(*a*) Tag–return data.

Cohort	Release year	Release age	No. of releases	No. of tag returns						
				1991	1992	1993	1994	1995	1996	1997
1990	1991	1	3299	20	40	46	23	13	5	4
	1992	2	4646		88	159	101	33	12	8
	1993	3	2777			66	78	32	17	15
1991	1992	1	2144		1	21	56	37	11	7
	1993	2	2937			60	68	67	21	11
	1994	3	3640				77	145	30	40
1992	1993	1	4898			2	41	201	91	58
	1994	2	3158				29	167	76	52
	1995	3	2629					55	103	74
1993	1994	1	9003				4	110	401	364
	1995	2	5899					83	395	363
	1996	3	1511						115	201
1994	1995	1	8585					0	87	622
	1996	2	2518						77	339
	1997	3	526							91

(*b*) Catch data.

Cohort	No. of fish caught						
	1991	1992	1993	1994	1995	1996	1997
1990	48 450	33 638	120 232	72 806	39 073	24 743	21 673
1991		7 624	38 414	119 166	61 080	38 646	27 398
1992			404	10 398	133 300	76 136	43 001
1993				187	30 789	171 859	72 177
1994					416	26 276	203 883

(*c*) Reporting rate estimates.

Cohort	Estimate						
	1991	1992	1993	1994	1995	1996	1997
1990	0.933	0.577	0.625	0.559	0.258	0.267	0.568
1991		0.887	0.750	0.600	0.388	0.250	0.537
1992			0.926	0.498	0.622	0.411	0.597
1993				0.522	0.592	0.474	0.639
1994					0.725	0.388	0.727

gest and oldest age of returns: $M_i = M_1 + (i - 1)[(M_5 - M_1)/4]$, where M_1 and M_5 are the two parameters to be estimated. By putting simple bound constraints on M_1 and M_5, we ensured that none of the mortality estimates could be negative.

The maximum likelihood parameter estimates and their estimated standard errors, obtained from the inverse Hessian matrix, are presented (Table 5). The M estimates decline from about 0.45 at age 1 to 0.05 at age 5 (noting that this was the lower bound). The F estimates are essentially zero at age 1, increase with age until age 3, then tend to decline to age 5. There was also a general increase in F within an age class over time. The P_1 estimates generally decline over time, from about 2.8 million age 1 fish for the 1990 cohort to between 1 and 1.5 million age 1 fish for the 1993 and 1994 cohorts.

The standard error estimates suggest CVs of about 20% for all P_1 estimates, 20%–30% for all F estimates, and 5% for M at age 1 (the age 5 value is not meaningful because the parameter converged to its lower bound). These are almost certainly too small because they do not take overdispersion of the data into account. Furthermore, if tagging mortality or tag shedding exist (and recent analyses suggest tag shedding is an issue for SBT), then there would be additional variance introduced in the parameter estimates, as well as bias (see Discussion).

The model has a large number of parameters being estimated (66) in relation to the number of data points (95). This brings up the issue of model selection and whether or not the parameter set could be reduced. For example, is it necessary to have 15 additional F^* parameters to allow for an initial period of nonmixing? Is it necessary to have age-specific M? Instead of having year- and age-specific fishing mortality rates, can F be modelled as a separable function with independent year and age factors (i.e., $F_{a,y} = F_a F_y$)? Model selection can be performed using likelihood ratio tests

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Table 5. Parameter estimates obtained by applying the integrated model to southern bluefin tuna (*Thunnus maccoyii*) data from several cohorts.

	Cohort				
Parameter	1990	1991	1992	1993	1994
M_1	0.464 (0.022)				
M_5	0.050 (0.001)				
F_1	0.019 (0.006)	0.003 (0.001)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
F_2	0.035 (0.007)	0.025 (0.005)	0.024 (0.005)	0.042 (0.007)	0.042 (0.009)
F_3	0.094 (0.017)	0.096 (0.018)	0.169 (0.025)	0.469 (0.140)	0.356 (0.069)
F_4	0.081 (0.015)	0.126 (0.027)	0.159 (0.035)	0.390 (0.095)	—
F_5	0.064 (0.017)	0.066 (0.018)	0.101 (0.020)	—	—
P_1	2.840 (0.520)	2.632 (0.514)	1.852 (0.333)	1.180 (0.237)	1.448 (0.343)

Note: Standard error estimates are given in parentheses. Data for the initial population size P_1 are in millions. Results were obtained using a coefficient of variation for the catch data of 0.30 and a standard error for the reporting rate estimates of 0.10. The λ and F^* parameter estimates are not of primary interest and are not shown. The M_1 and M_5 estimates apply to all cohorts.

or, more commonly in wildlife applications, using Akaike's Information Criterion (AIC) (Akaike 1974). While we stress that performing model selection to find the most parsimonious model is an important part of any analysis, it is not the focus of this paper, and so we did not carry out an exhaustive model selection procedure for the SBT data. We did, however, test the necessity of including separate Fs in the year of tagging. The AIC value for the model including separate Fs was more than 110 units smaller than the AIC for the model without separate Fs, which suggests that an initial period of nonmixing does in fact exist and should be allowed for in the model. The residuals (not shown) were much improved in the model with separate Fs as well. We also found that fitting the model with a constant M at all ages resulted in only a small increase (1.6) in the negative log-likelihood value, suggesting the fit is equally good according to AIC. The estimate of M in this model was 0.44, meaning much larger M at older ages than the linear model predicted; as a result, the estimates of F at older ages increased. These results reinforce the well-known difficulties with estimating M, the high correlation between M and F, and the need to take caution when interpreting results. On a positive note, the population size estimates were highly robust with respect to the model assumed for natural mortality.

Further work needs to be conducted before drawing any conclusions regarding these estimates for SBT. We have discussed the need to perform more comprehensive model selection and have shown the sensitivity of the results to assumptions made about natural mortality. In addition, consideration needs to be given to alternative reporting rate estimates and to the incorporation of tag shedding. Our purpose here was to illustrate the ability of the integrated tagging and catch model to provide estimates of both mortality rates and abundance using real data, not to provide a comprehensive analysis for SBT. Nevertheless, the results do suggest that SBT have quite high juvenile natural mortality rates for such a long-lived fish. In addition, the decrease in recruitment estimates and the relatively high F estimates suggests that the data may be providing important indicators with respect to the status of the stock and fishery.

As an aside, we calculated a profile of the negative log-likelihood for the catch CV and confirmed that as expected from previous discussions, the global minimum in the negative log-likelihood occurs near zero (Fig. 3*a*). In this case, there is not another local minimum elsewhere. However, we found that when the reporting rate estimates are assumed to be known without error (increasing the relative influence of

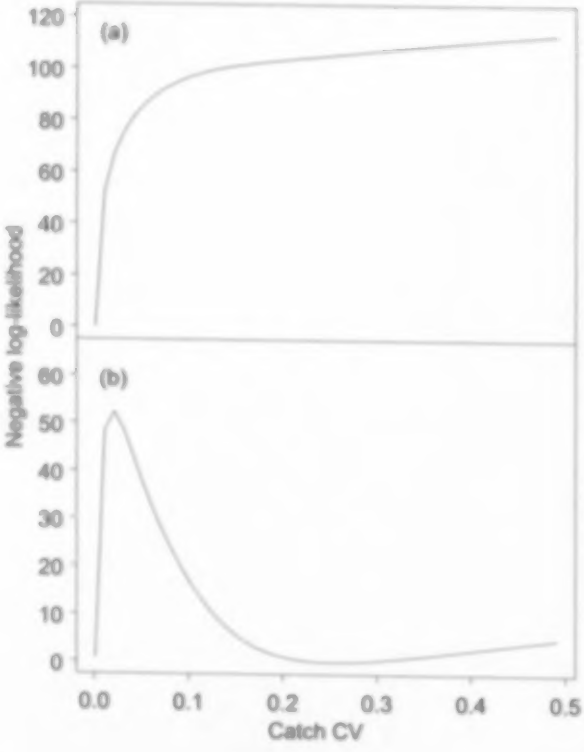

Fig. 3. Negative log-likelihood profile for the coefficient of variation (CV) of the catch data for southern bluefin tuna (*Thunnus maccoyii*) when the model (*a*) allows for error in the reporting rates and (*b*) assumes the reporting rates are known without error. The negative log-likelihood value is plotted as the difference from the minimum value.

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the tag–recapture data in the overall likelihood), then the profile changes dramatically (Fig. 3*b*). There is still a global minimum near zero, but a local minimum also occurs around 0.25. This suggests that our initial choice of 0.30 for the catch CV was reasonable, but it also reinforces that this parameter cannot be reliably estimated by the model.

Discussion

We have developed a comprehensive framework for modelling data from multiyear tagging experiments in a fishery context that incorporates catch data. Integrating multiyear tagging data and catch data results in a synergy between the two data sets in that it provides an estimate of the initial population size, which cannot be obtained from the multiyear tagging data alone (i.e., from a Brownie-type experiment). This method also provides estimates of mortality rates, which cannot be obtained from single release tagging data and catch data alone (i.e., from a Petersen-type experiment). Additionally, incorporating catch data into the tagging model improves the mortality rate estimates (especially F). Our simulation results suggest that including catch data can improve the accuracy of F estimates substantially (up to 60%) and also decrease biases, especially in the M estimates. Of course, the degree of improvement depends on the situation and is greatest when the catch data are known precisely and, to a lesser extent, when the number of tag releases is small.

The large biases observed in many of the mortality rate estimates at low numbers of releases were unexpected given that biases in estimates from Brownie-type models have not, to our knowledge, been highlighted in the literature. We were expecting the mean estimates to be relatively unbiased regardless of whether catch data were included; instead, biases were present for both models but were slightly smaller in the model with catch data. The reason for the biases is not completely understood; however, they most likely stem from the fact that the M and F estimates are highly correlated and also that the model is highly parameterized (both issues are discussed below). Nevertheless, with larger number of releases, these biases become small.

High correlations were present among many parameter estimates and are expected with the model formulation being used. In particular, positive correlations between the M and F estimates, especially at older ages, are expected because an increase in M means that less fish are still alive in the population, so to achieve a particular level of catch and tag returns, F must increase. For the same reason, the Fs between ages and fisheries are often highly positively correlated. For example, an increase in F at a given age means less fish are alive at subsequent ages, so to achieve a particular level of catch and tag returns at these older ages, F must increase. Finally, negative correlations between the initial population size and the F estimates are often present because to achieve a particular level of catch, the population size must have been larger if F had been low than if F had been high.

In our simulations, we considered a tagging experiment involving a single cohort of fish, and we allowed F and M to differ at each age (to the greatest extent possible). This resulted in a highly parameterized model. In practice, it is likely that two or more cohorts would be tagged in a given year, as was done in the case of SBT tagging experiments. If any parameters are the same between cohorts, then including more cohorts will make the model more parsimonious and improve parameter estimation. For example, we redid the simulations that assumed 250 releases at each age, ϕ of 3, and a catch CV of 0.10, except we generated data for two cohorts instead of one. In applying the model, we allowed for F to differ with age and cohort, but for M to differ only by age (keeping it the same across cohorts). The large biases that were present in the M estimates with one cohort disappeared, and the bias in F_3 more than halved. Furthermore, the CV of the F_3 estimate decreased by about 25%, and the CVs of the M_1 and P_1 estimates decreased by about 10%.

Our model assumes no tag-induced mortality or tag shedding. If either exists, then the parameter estimates would have additional variance, and moreover, they would be biased if these factors were not accounted for. Auxiliary information needs to be collected to allow for their estimation. There has been extensive work on approaches for estimating these quantities, especially tag shedding from double-tagging experiments (e.g., Beverton and Holt 1957; Kirkwood and Walker 1984; Barrowman and Myers 1996). We also note that if heterogeneity exists among taggers, then using a simple average rate for tag shedding and tagging mortality over all taggers can induce substantial biases to the parameter estimates of interest (Hearn et al. 1991).

Like most published Brownie-type models, our model also assumes that the ages at tagging are known without error. If aging errors exist, then biases can be introduced in the parameter estimates. Whether or not this is a serious issue will be highly case-specific, depending on the accuracy of the method used to determine ages as well as on the underlying dynamics of the species (for example, if mortality rates are similar across ages, then age misclassifications are less important). However, it is shown in Polacheck et al. (2006) that the effects of aging errors on mortality rate estimates from a Brownie model are expected to be minimal in many situations.

Incomplete mixing of tagged animals within the full population and heterogeneity in the capture probabilities is the most challenging problem confronting the use of tagging experiments. These factors can introduce increased variance as well as biases into the parameter estimates and are probably the biggest limitation in the application of tagging experiments in fisheries. We classify incomplete mixing into two basic types: systematic and unsystematic. Unsystematic incomplete mixing refers to situations where there is still a large degree of mixing between tagged and untagged fish, and the pattern of mixing has a large random component, such that on average, the probability of capture is the same for tagged and untagged fish. This is the type of nonmixing referred to in the Overdispersion in the tag–recapture and catch data section, and although it should not bias the parameter estimates, it will result in overly optimistic standard error estimates. We already mentioned possible ways of obtaining more realistic variance estimates, including bootstrapping and using modified estimation models and methods. We also mentioned the possibility of postestimating the amount of overdispersion and inflating the standard error es-

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timates derived from Hessian accordingly. However, in our simulation results, we saw that the amount the standard error estimate needs to be inflated can differ among parameters and does not always have an obvious relationship with the level of overdispersion.

Systematic incomplete mixing refers to the situation where there is a systematic and repeatable pattern of nonmixing between tagged and untagged fish — for example, if all tagging was done late in the season in one location and fish in that location and time period only remain in one part of the stock's overall range. Such systematic nonmixing will induce biases into the population and mortality estimates if not accounted for within the estimation model. When incomplete mixing results from a high degree of site fidelity within the geographic range of the population, it may be necessary to include a spatial component within the analysis. In this case, there is no universal solution and the most appropriate approach will depend on the specifics of the population.

In all tagging experiments, strategies can and should be used to avoid and minimize the effect of incomplete mixing, both in the design of the releases or in the analysis of the return data. For example, to the greatest extent possible, it is important to spread tagging effort throughout the area where fish are found. In cases where tagging occurs around the same time as peak catches (which is likely, since that is usually the time when fish are most available), it is important to allow for a period of nonmixing. A method for incorporating nonmixing in the first year has been developed for Brownie-type models (Hoenig et al. 1998*b*) and, as we illustrated in our application to SBT data, can easily be extended to the Brownie model with catch data developed here. If the period of nonmixing is less than a year, then precision in the parameter estimates can be gained by modifying the model to only allow for nonmixing in part of the first year.

Similarities exist between the methods and likelihood function developed here and those developed for use in integrated statistical catch-at-age or size stock assessment models involving tagging data (e.g., Fournier et al. 1998; Kolody and Polacheck 2001; Butterworth et al. 2003). However, we are not aware of any integrated stock assessment models that have incorporated a Brownie-type estimator for the tagging data (although it would be relatively straightforward to do so). Even so, there are important distinctions between these integrated stock assessment models and the integrated tagging and catch model presented here. Integrated stock assessment models attempt to estimate the entire age structure and history of a population since the beginning of exploitation. The models are overparameterized and various assumptions (particularly with respect to catchability and selectivity) are required to yield an identifiable set of parameters. These can involve various penalty terms, and the results are frequently sensitive to alternative assumptions and to relative weights given to the penalty terms and data components of the objective function. Simply improving the precision of the data will not necessarily improve the reliability of the estimates or the structural features (e.g., penalty functions) of the model. On the other hand, the integrated tagging and catch model allows for all parameters to be estimated (with the exception of M at older ages) without requiring any assumptions about selectivity and catchability. As a result, the model can be used to test a suite of assumptions with regard to the parameters, such as whether fishing mortality can adequately be described using a selectivity function or whether certain parameters are common between ages or years. Furthermore, the integrated tagging and catch model can be used to directly evaluate the trade-off in the amount of resources placed into the different data collection components. Of course, a disadvantage is that estimates are only possible for cohorts and ages for which tagging data are available. In this context, we see the integrated tagging and catch model as complementary to stock assessment models.

Another feature of the integrated tagging and catch model is that it does not rely on the use of catch per unit effort (catch rate) or standard effort data. These data form an essential component of many stock assessments (i.e., those without fishery-independent surveys or tagging), but are also one of the more uncertain and unreliable components. Tagging can provide a useful alternative to catch rate and effort data and are perhaps the only viable alternative in a number of fisheries where fishery-independent surveys are not possible. Admittedly, tagging experiments involve a number of complications and assumptions of their own. Ensuring that the tagging experiment (both the release and recovery components) are well designed and executed is critical to avoid situations that would render the data as uncertain and unreliable as catch rate data. However, unlike catch rate data, many of the uncertainties associated with tag–recapture data can be minimized through well-designed and implemented tagging experiments and comprehensive analysis methods. Moreover, the data themselves can be used to test for violations of the critical assumptions.

Ultimately, the tagging and catch likelihood components developed here may be incorporated into an integrated statistical stock assessment. However, an independent analysis of only the tagging and catch data is important because it provides estimates of critical parameters that are not confounded by the structural assumptions of the stock assessment models and also allows for testing of these assumptions. Furthermore, it provides a means to check for consistency between the tagging and catch data themselves as well as between these data sets and other data sets used in the assessment. To this end, it is desirable to carry out a variety of independent analyses using different data components to cross-check model assumptions and consistency of data sets. Such checks should be done as a standard part of any assessment to ensure the robustness of the conclusions. If inconsistencies are found, it is important to develop and incorporate a range of hypotheses and not simply "average-out" the discrepancies.

Overall, the results from this paper demonstrate the potential for combining multiyear tagging data with catch-at-age data to provide reliable estimates of the population parameters of interest for stock assessments. High levels of precision can be obtained for the fishing mortality and abundance estimates as long as sufficient resources are devoted to tag releases and estimation of the catch-at-age data. While the precision of the M estimates is much lower, tagging experiments provide perhaps the only mechanism to circumvent the need to assume values for M, which is inherent in most catch-at-age stock assessments. In many cases, they also provide the only alternative to using fishery-dependent catch and effort data for "tuning" these assessments. Without be-

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ing a panacea to the estimation problems facing stock assessments, tagging experiments are a potentially powerful tool that deserve more consideration within research programs for improving and augmenting traditional stock assessment approaches.

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Appendix A

The notation and parameterizations used in this appendix were chosen to be illustrative of the model in the main body of this paper. Thus, in the presentation below, N represents the number of tag releases at a particular age, $R_1,\ldots,R_{k-1}$ represent the number of tag returns at ages 1 to $k-1$, and R_k represents the number of tags that were not returned by age k. The πs are the random Dirichlet probabilities of return at age and the ps are their expected values.

The Dirichlet distribution

The Dirichlet distribution is used to describe the variation in a set of proportions that sum to 1. The probability density of a set of proportions $\underline{\pi} = (\pi_1,\ldots,\pi_k)$ with parameter set $\underline{p} = (\omega, p_1,\ldots,p_k)$ is given by

$$\Pr(\underline{\pi}) = \frac{\Gamma(\omega)}{\prod_{i=1}^{k}\Gamma(\omega p_i)}\prod_{i=1}^{k}\pi_i^{\omega p_i - 1}$$

where $0 < p_i < 1$ for all i and $\sum_{i=1}^{k} p_i = 1$. The mean and variance of the proportions are $E(\pi_i) = p_i$ and $V(\pi_i) = p_i(1 - p_i)/(\omega + 1)$. Note that the Dirichlet distribution with $k = 2$ reduces to the beta distribution.

The Dirichlet–multinomial distribution

The multinomial distribution describes a situation in which N independent random trials are conducted and the outcome of each trial can fall into one of k categories. The probability of falling into category i is π_i ($\sum_{i=1}^{k}\pi_i = 1$). The final category counts $\underline{R} = (R_1,\ldots,R_k)$, where $\sum_{i=1}^{k} R_i = N$, have a multinomial distribution with probability density

$$\Pr(\underline{R}) = \frac{N!}{\prod_{i=1}^{k} R_i!}\prod_{i=1}^{k}\pi_i^{R_i}$$

When the category probabilities are themselves viewed as random variables following a Dirichlet distribution, then the multinomial probability density given above describes the conditional distribution of the category counts given the probabilities, which we denote by $\Pr(\underline{R}|\underline{\pi})$. Then the unconditional distribution of the category counts is given by the compound distribution called the Dirichlet–multinomial with probability density

$$\Pr(\underline{R}) = \int_{\underline{\pi}} \Pr(\underline{R}|\underline{\pi})\Pr(\underline{\pi})\,d\underline{\pi}$$

The integral is k-dimensional over all values of $\underline{\pi}$ such that $0 \le \pi_i \le 1$ and $\sum_{i=1}^{k}\pi_i = 1$. It is easy to show that the resulting distribution is

$$\Pr(\underline{R}) = \frac{N!}{\prod_{i=1}^{k} R_i!}\prod_{i=1}^{k}\frac{\Gamma(R_i + \omega p_i)}{\Gamma(\omega p_i)}$$

The mean and variance of the category counts are $E(R_i) = Np_i$ and $V(R_i) = \phi Np_i(1 - p_i)$, where $\phi = (N + \omega)/(\omega + 1)$. Thus the variance for Dirichlet–multinomial data is a factor of ϕ times larger than multinomial counts, and we will refer to ϕ as the overdispersion factor.

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A field study examining the relative importance of food and water as sources of cadmium for juvenile yellow perch (*Perca flavescens*)[1]

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Abstract: To determine the relative importance of water and food as cadmium (Cd) sources for juvenile yellow perch (*Perca flavescens*, age 1+), fish were caged for up to 30 days in either a reference (Opasatica) or a Cd-contaminated (Dufault) lake and offered prey (zooplankton) from one of these lakes. We established four Cd-exposure regimes: a control, Cd-contaminated water only, Cd-contaminated food only, Cd-contaminated food and water. The 64 µm mesh cages used allowed the free exchange of water with the surrounding lake while retaining the added zooplankton prey for the perch. Cd in the gills and kidney of caged perch was taken up largely from lake water, whereas liver and gut Cd appeared to come from both dietary and aqueous sources. At the subcellular level (liver), the majority of the background Cd in control perch was associated with metal-sensitive fractions (organelles and heat-denatured proteins), whereas in perch exposed to waterborne or diet-borne Cd, the majority of the Cd was found in a metal-detoxified fraction (heat-stable proteins, metallothionein). For perch from all treatment levels, the higher the concentration of hepatic Cd, the greater the proportion of the Cd burden in this organ that was associated with the fraction containing metallothionein-like proteins.

Résumé : Afin de déterminer l'importance relative de l'eau et de la nourriture comme sources du cadmium (Cd) pour la perchaude (*Perca flavescens*, âge 1+), des spécimens juvéniles provenant d'un lac de référence (lac Opasatica) ont été exposés pendant 30 jours dans des cages installées soit dans leur lac d'origine, soit dans un lac contaminé par le Cd (lac Dufault) et nourris de proies (zooplancton) venant d'un des deux lacs. Nous avons établi quatre traitements : témoin, exposition au Cd via l'eau seulement, exposition au Cd via la nourriture seulement et exposition au Cd via l'eau et la nourriture. La maille des cages (64 µm) était assez petite pour retenir le zooplancton fourni comme proies, tout en permettant l'échange de l'eau entre les cages et le lac environnant. Le Cd qui s'accumulait dans les branchies et le rein provenait essentiellement de l'eau, alors que le Cd accumulé dans le tractus intestinal et le foie provenait à la fois de l'eau et de la nourriture. Au niveau hépatique subcellulaire, la majorité du Cd était associé aux fractions potentiellement sensibles au métal (organelles et protéines sensibles à la chaleur) chez les témoins non-exposés, alors qu'il se trouvait dans la fraction détoxiquée (protéines stables à la chaleur, métallothionéine) chez les poissons exposés à l'eau ou à la nourriture contaminée. Pour tous les traitements où l'eau ou la nourriture était contaminée, la proportion du Cd associé à cette fraction détoxiquée augmentait avec les teneurs hépatiques totales en Cd.

Introduction

In nature, fish are exposed to trace metals through both ambient water and food. For the nonessential metal cadmium (Cd), there is a lack of consensus regarding the relative importance of these two metal sources. For example, for freshwater fish, various investigators have concluded that dietary and aqueous sources are important (Farag et al. 1994; Kraal et al. 1995), that water is the main route of exposure (Williams and Giesy 1978), or that these animals receive the majority of their Cd from food (Dallinger and Kautzky 1985; Harrison and Klaverkamp 1989; Mount et al. 1994). This lack of agreement among researchers can be explained, in part, by differences in experimental design. Most studies have been carried out in the laboratory, where experimental artefacts are difficult to avoid. For example, it is difficult to expose fish to metals in food alone because the metal can desorb or leach from contaminated food and thus be available for uptake by the fish from water. Furthermore, some researchers have used artificial, Cd-spiked diets (Williams and Giesy 1978; Harrison and Klaverkamp 1989; Handy 1993) from which fish are likely to assimilate Cd differently than they would from naturally contaminated prey.

To avoid the complications inherent in using artificially contaminated diets, other researchers have measured the importance of dietary Cd using live prey (Mount et al. 1994;

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Kraal et al. 1995). However, these live prey are often exposed to metals at unrealistically high concentrations for a short period of time in water only; in the field, metals in the prey come from the ambient water and via the trophic chain. A more realistic laboratory exposure scenario involves the use of naturally contaminated invertebrates collected from the field as food for fish (Farag et al. 1994; Woodward et al. 1995). The advantage of this approach is that prey have been exposed to metals in nature over their life-span, which is important because metals in the soluble fraction within prey cells tend to be more readily available to predators than metals associated with particulate fractions (Wallace and Lopez 1996; Wallace et al. 1998).

In the present study, we sought to avoid the artefacts associated with laboratory studies and instead conducted a field experiment to quantify the relative importance of water and food as Cd sources for juvenile yellow perch (*Perca flavescens*; hereafter referred to as perch). We chose this species of fish because perch are found in both pristine and metal-contaminated lakes, and they have been the subject of several earlier field studies examining both metal accumulation and detoxification (Levesque et al. 2002; Eastwood and Couture 2002; Giguère et al. 2004). We also examined the hepatic subcellular partitioning of Cd to learn how fish cope with the influx of this nonessential metal. We used a fractionation procedure to separate the Cd bound to physiologically sensitive fractions (such as enzymes and organelles) from the metal tied up with metal-binding proteins, such as metallothionein, which are thought to play an important role in metal detoxification.

Materials and methods

Study area

Lakes Opasatica and Dufault are located approximately 600 km north of Montréal, close to the city of Rouyn-Noranda in northwestern Quebec, Canada. Sources of metal contamination in this area include mining and smelting operations, as well as mineralized outcrops. A copper smelter has been in operation within the city of Rouyn-Noranda since 1927. Lake Dufault (48°20′N, 79°0′W) is situated close to the smelter (distance of ~2 km) and exhibits elevated levels of metals such as Cd, copper (Cu), and zinc (Zn) (Giguère et al. 2004). The reference lake used in our study (Lake Opasatica; 48°5′N, 79°20′W) is located ~30 km upwind of the smelter and has relatively low concentrations of these trace metals.

The enclosures

Juvenile perch (1.5 ± 0.1 g; mean ± standard error, SE) were collected from Lake Opasatica on 8 June 2003 (water temperature: 11 °C) and placed in cages located in both Lake Opasatica (two cages per treatment group) and Lake Dufault (two cages per treatment group; water temperature: 12 °C). Each cylindrical cage (height 1.2 m, diameter 0.5 m) was made of Nitex netting (64 µm mesh aperture) topped by Styrofoam flouts and anchored to the lake bottom (Munger et al. 1999). The flouts held the cage opening well above the surface to prevent zooplankton from entering by wave action. Each cage initially contained 10 fish.

The cages were filled by passive entry of lakewater through the netting, which prevented the entry of macrozooplankton. Perch were allowed to acclimate to their cages for 24 h and were not fed during this time period. The caged fish in both lakes were then fed daily with macrozooplankton collected from either the reference lake or the Cd-contaminated lake, creating four treatment regimes: reference lakewater and reference diet (REF), reference lakewater and contaminated food (FO), contaminated lakewater and reference food (WO), and contaminated lakewater and contaminated food (WF). Two individual cages were set up for each sampling time (15 and 30 days) and for each treatment (REF, FO, WO, WF) giving a total of 16 cages. To reduce stress and to minimize the effect of changes in population density, fish from these cages were not serially sampled over time. Instead, at each sampling time, two cages from each treatment were removed and all the fish from these cages were collected for analyses. Fish sampled after 15 and 30 days of exposure were sacrificed and the gills, gastrointestinal tract (gut), kidney, and liver were analyzed for Cd. Juvenile indigenous perch from both lakes were also collected for metal analyses on days 0, 15, and 30.

Zooplankton to be offered as prey for perch were collected by towing a plankton net (64 µm mesh aperture) in the top 2 m of both study lakes. These prey were stored live in 10 L, high-density, polyethylene bottles for <2 days and fed to fish daily. Perch were fed a ration of approximately 10% of their body weight per day. We estimated the volume of water (and prey) that we needed to attain this ration by determining the weight of zooplankton in a 100 mL subsample from one of the 10 L bottles. To reduce the quantity of Cd-contaminated water being added with contaminated prey to cages in the reference lake, zooplankton were concentrated into <100 mL of lakewater prior to being offered to the fish. To minimize prey mortality, zooplankton offered to the fish were never exposed directly to air, but were concentrated by slowly filtering the samples through a bottomless 100 mL bottle fitted with Nitex netting (64 µm) over the opening. To get an estimate of how quickly zooplankton were consumed by perch, the cages were subsampled using a 5 cm diameter plastic tube, the length of which was approximately equal to the depth of the cage. With this tube, water samples were collected vertically from several locations within a cage until a total of 1 L of water had been collected. Zooplankton were then counted in this 1 L sample, both immediately after feeding, up to an hour post-feeding and then again the next day before feeding. When zooplankton were added to the cages, perch began feeding actively. Zooplankton samples taken within the cages revealed that the majority of the zooplankton was eaten within 1 h and that almost no zooplankton remained after 24 h.

To monitor aqueous Cd in the cages receiving Cd-contaminated prey in the reference lake, we used Plexiglas in situ diffusion samplers suspended in these cages. These samplers were acid-washed (15% HNO_3) and rinsed with MilliQ (>18 Ω) water prior to use. They were then filled with MilliQ water and covered with a 0.2 µm nominal pore size Gelman HT-200 polysulphone membrane. Once assembled, the diffusion samplers were placed in the water column on days 3, 18, and 26 where they were allowed to equilibrate for 3 days within the cages to achieve a steady state with the

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ambient lakewater. Plexiglas samplers were also placed outside the cages in each lake to measure ambient Cd concentrations. Free Cd^{2+} ion concentrations were estimated for the two study lakes with the Windermere Humic Aqueous Model (WHAM 6.0; Tipping 1998) using concentrations of total dissolved Cd, inorganic ligands (e.g., chloride, sulphate, and carbonates), and organic carbon (C) as input data.

Fish mortality

In preliminary field trials, we noted high mortality if perch were caught and transported during the summer months when the water was warm (~18–20 °C). To minimize perch mortality, we started the experiments in early June when the water temperature was low (~11 °C). Although we believe that cooler water did help reduce mortality, some fish still died during the experiment (90 of 160 fish were recovered). When dead fish were seen in the cages, they were removed and the feeding ration was adjusted accordingly. Because there was some predation by birds, the exact number of surviving fish was only known with certainty at the end of the experiment.

Metal analyses

After 15 and 30 days of Cd exposure, perch were removed from the cages, dissected, and Cd was measured in the gills, gut, kidney, and liver. Similarly, juvenile indigenous perch were collected on days 0, 15, and 30 from both Lake Dufault and Lake Opasatica. The gills and gut were chosen for analysis, as they are important organs for Cd exchange between perch and their environment, whereas the kidney and liver were chosen because of their importance as organs for Cd storage. To minimize trace metal contamination, organ samples were stored in acid-washed (15% HNO_3) Eppendorf polypropylene tubes. Liver samples used for subcellular analyses (outlined below) were stored in liquid nitrogen (N_2) until homogenization. The other organs were lyophilized, weighed, and then digested in 70% HNO_3 (~3 mL acid·g^{-1} dry weight of organ). Digestions were carried out in screw cap Teflon bottles in an autoclave (120–125 °C, 1.1–1.3 kg·cm^{-2}, 3 h). During each digestion run, both blanks (HNO_3 and MilliQ water) and certified reference samples (lobster hepatopancreas (TORT-2); National Research Council of Canada, Ottawa, Ontario) were included. Samples were analyzed for Cd by inductively coupled plasma atomic emission spectrometry (Varian Vista AX, Varian Inc., Mulgrave, Victoria, Australia). Low to negligible contamination was detected in the digestion blanks (N = 6). Certified samples were quantitatively recovered (N = 6): Cd, 93% ± 10% (mean ± SE).

Differential centrifugation

For subcellular analyses, liver samples were removed from liquid N_2 and gently thawed and homogenized in two volumes of cold 0.9% NaCl in a glass Potter–Elvehjem homogenizer. Homogenates were transferred to 1.5 mL Eppendorf polypropylene tubes in which they were subjected to a differential centrifugation protocol adapted from Wallace et al. (2003). First, homogenates were centrifuged at 800*g* for 15 min at 4 °C. This step produced a supernatant containing organelles and proteins and a pellet containing cellular debris. The supernatant from this first spin was then subjected to an ultracentrifugation at 100 000*g* for 60 min at 4 °C, producing a pellet containing organelles. The resulting supernatant was then heat-denatured at 80 °C for 10 min followed by placement on ice for 1 h. Following this denaturation step, the supernatant was centrifuged at 50 000*g* for 10 min at 4 °C to produce a pellet containing heat-denaturable proteins (HDP) such as enzymes and a supernatant containing heat-stable proteins and peptides (HSP) such as glutathione and metallothionein-like proteins. Thus, four fractions were obtained from this centrifugation procedure: cellular debris, organelles, HDP, and HSP.

Pellets from the centrifugation procedure were lyophilized and digested in 70% HNO_3 for 5 days at room temperature, after which they were diluted to 2% HNO_3 with ultrapure water. As the supernatants only contained dissolved peptides and proteins with relatively little extraneous organic matter, they were not digested but rather were simply acidified to 2% HNO_3. Metal concentrations in the subcellular fractions were analyzed by inductively coupled plasma – mass spectrometry (Model X-7; Thermo Electron Corp., Waltham, Massachusetts). Blanks and a certified reference material (TORT-1; National Research Council, Ottawa, Ontario) were digested in the same manner. Blanks indicated negligible contamination (Cd < 0.013 μg·L^{-1}), and the recoveries of Cd in TORT-1 reference samples (N = 4) were 96% ± 8% (mean ± SE).

To obtain a measure of total liver Cd, an aliquot of the homogenate was taken for analysis before the first centrifugation step. This aliquot was also used in a mass balance calculation to verify the recovery of Cd in the various subcellular fractions. The average recovery of Cd was 107% ± 4% (N = 13; mean ± SE).

Statistical analyses

In previous field transplant experiments (Kraemer et al. 2005), we observed that Cd accumulation in the liver and kidney was relatively slow; substantial changes in hepatic and renal Cd concentrations were only detected after 10–20 days. Therefore, for the current diet manipulation experiment, we concentrated on the day 30 exposure data set to evaluate the contributions of water and diet to Cd accumulation in various organs.

For the liver, gut, and kidney data sets, the conditions of normality (examined with a Kolmogorov–Smirnov test) and homogeneity of variance (examined with a Levene Median test) were met. Using the day 30 data set, we initially partitioned the variance among the organ (gut, liver, and kidney) and Cd treatments (REF, FO, WO, WF) with a two-way analysis of variance (ANOVA). Organ and treatment factors and organ × treatment interactions were highly significant (P < 0.001). Given that organ concentrations varied differently within treatments, and since we were directly interested in the effect of Cd source (treatment) on each organ, the data were reanalyzed using 1-way ANOVA and a posteriori multiple comparisons were examined with the Tukey–Kramer honestly significant difference test ($P \leq 0.05$). Owing to violations in normality, the nonparametric Kruskal–Wallis test was used for the gill data set and multiple comparisons were examined with Dunn's post hoc test ($P \leq 0.05$).

Cd concentrations in the indigenous fish from lakes Opasatica and Dufault were also compared at t = 30 days us-

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Table 1. Mean aqueous cadmium concentrations [Cd] (± standard error; $N = 4$) within cages located in Lake Opasatica sampled after 6, 21, and 29 days of feeding yellow perch (*Perca flavescens*) with a Cd-contaminated diet.

Lake	Sample	[Cd] (nmol·L^{-1})	[Cd^{2+}] (nmol·L^{-1})
Opasatica	Cage receiving Cd-contaminated food; 6 days	0.12±0.003a	
	Cage receiving Cd-contaminated food; 21 days	0.13±0.009a	
	Cage receiving Cd-contaminated food; 29 days	0.39±0.036b	
	Cage receiving reference diet; 6 days	0.10±0.005a	
	Lakewater outside the cages	0.11±0.021a	0.02*
Dufault	Lakewater	5.55±0.028c	2.48*

Note: Also given are total aqueous Cd and calculated free Cd^{2+} concentrations in both lakes. Aqueous Cd concentrations followed by the same letter are not significantly different (one-way analysis of variance followed by Tukey–Kramer post hoc test; $P \leq 0.05$).

*Free Cd^{2+} concentrations were estimated using the Windermere Humic Aqueous Model (WHAM 6.0.1; Tipping 1998).

ing a 2-way ANOVA (lake and organ as factors). Both main effects and the lake × organ interaction were highly significant ($P \leq 0.001$). Since we were interested in organ differences between lakes, we reanalyzed the data with the Student's *t* test, comparing Lake Opasatica with Lake Dufault for each organ.

For the subcellular analyses, we first compared Cd concentrations in the subcellular fractions in perch that had received Cd from different sources for 30 days. Using a similar approach as for the whole-organ data sets, differences in Cd concentrations in the subcellular fractions (organelles, HDP, HSP, and cellular debris) resulting from Cd exposure from different sources (FO, WO, and FW) were examined with a 2-way ANOVA (using Cd source and subcellular fractions as factors) for the day 30 data set. Statistical analysis was performed on all experimental data with SYSTAT 10 and SigmaStat 3.11 (SPSS Inc., Chicago, Illinois, USA).

Results

Cd in the reference and metal-impacted lakes

The contamination status of our two study lakes was confirmed by the fact that calculated free Cd^{2+} ion concentrations in the metal-impacted Lake Dufault were ~130 times greater than those in the less-impacted Lake Opasatica (Table 1). Likewise, Cd concentrations in zooplankton from the metal-impacted lake were significantly higher than those in zooplankton collected from the reference lake (see Table 2). In indigenous perch, Cd concentrations were also significantly ($P \leq 0.001$) higher in all the organs examined for individuals collected from metal-impacted Lake Dufault than in those from the reference lake (Figs. 1 and 2). Cd concentrations differed among organs and decreased in the following order: kidney > liver > gut > gills.

Since fish receiving Cd-contaminated food also received a small volume (<100 mL) of Cd-contaminated water from Lake Dufault, we tested if this addition significantly increased aqueous Cd concentrations in these cages. Aqueous Cd concentrations in cages where fish received Cd-contaminated food only were measured after 6, 21, and 29 days of experimentation. These values were compared with ambient aqueous Cd concentrations in lakes Opasatica and Dufault (one-way ANOVA, Tukey–Kramer post hoc tests, $P \leq 0.05$). The addition of Cd-rich prey collected from Lake Dufault to cages in Lake Opasatica did not lead to an appreciable increase in dissolved Cd in the cages located in this reference lake (Table 1); the small amount of contaminated water added with prey was thus insufficient to influence Cd uptake by the perch.

Table 2. Mean cadmium concentrations [Cd] (± standard error; $N = 3$) in bulk zooplankton samples collected from Lakes Opasatica and Dufault in June and July.

Lake	Month	[Cd] (μg·g^{-1} dry weight)
Opasatica	June	4.9±0.3
	July	2.8±0.2
Dufault	June	10.2±0.9***
	July	11.8±0.3***

Note: Concentrations were compared between lakes for each month with the Student's *t* test, and significant differences between lakes ($P \leq 0.001$) are represented by asterisks (***).

Cd in the organs of caged perch

Owing to mortality, fish from replicate cages (two cages for each sampling time and each exposure treatment) were pooled to have enough tissue for analyses. After 30 days of exposure to Cd, both the gut and liver were mainly influenced by aqueous Cd, but diet-borne Cd also contributed to the bioaccumulation (Figs. 1*a*, 2*a*). Cd concentrations in both the gut and liver of perch exposed only to dietary Cd for 30 days were significantly higher than those concentrations measured in Lake Opasatica perch (Student's *t* test; $P \leq 0.01$). By the end of the experiment, concentrations in the gut of caged fish exposed to aqueous Cd either alone or with the Cd-contaminated diet were not significantly different from those in indigenous Lake Dufault perch (Student's *t* test; $P > 0.05$). This was not the case for the liver, as hepatic Cd concentrations in caged fish were still significantly lower than those in indigenous Lake Dufault perch, indicating that unlike the gut, steady state had not yet been achieved in this organ ($P \leq 0.001$).

Unlike the liver and the gut, there appeared to be no significant influence of dietary Cd on bioaccumulation in the gills and kidney; after 30 days of exposure, Cd concentra-

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Fig. 1. Temporal changes in cadmium (Cd) concentrations in the gut (*a*) and gills (*b*) in caged yellow perch (*Perca flavescens*) receiving Cd from the reference diet + reference water (reference), Cd-contaminated diet + reference water (food only), reference diet + Cd-contaminated water (water only), and Cd-contaminated food + water (food and water). Also shown are Cd concentrations in indigenous yellow perch sampled on days 0, 15, and 30 from Lakes Opasatica (solid bars) and Dufault (open bars). All statistical analyses were carried out on the 30 day data set. Comparisons between indigenous yellow perch from Lakes Dufault and Opasatica are represented by an asterisk (*; $P \leq 0.001$); significant differences in Cd concentrations in caged fish are represented by different letters ($P \leq 0.05$). On day 30, $N = 1$ (# symbol) for the reference fish.

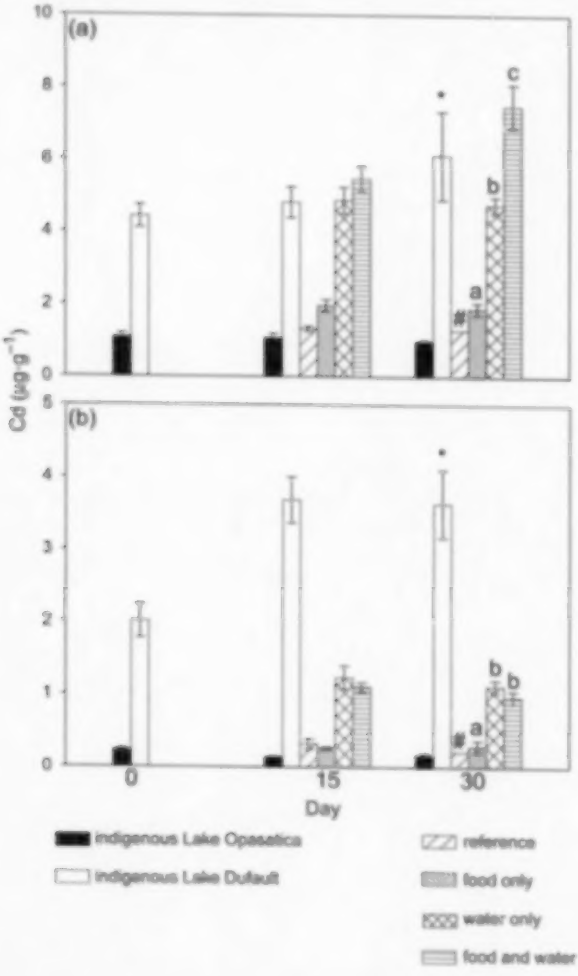
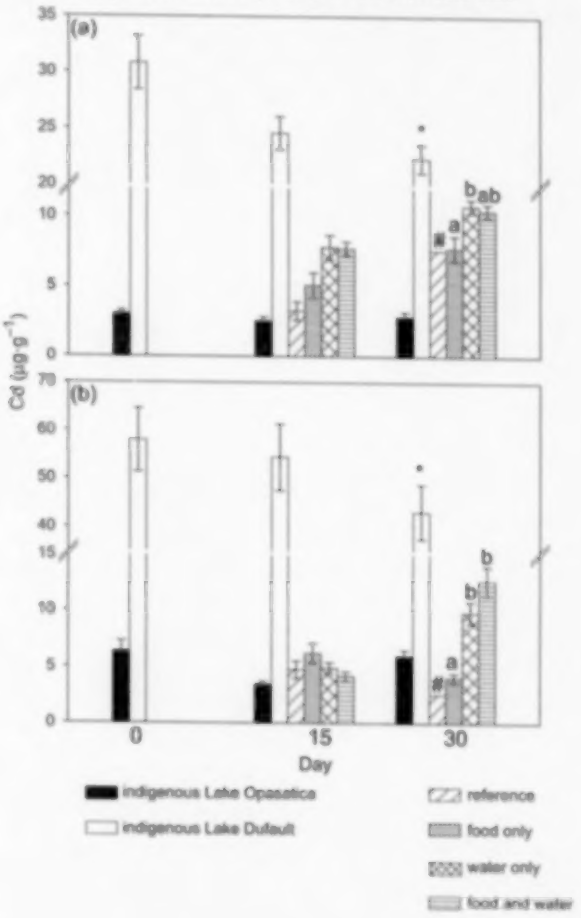


Fig. 2. Temporal changes in cadmium (Cd) concentrations in the liver (*a*) and kidney (*b*) in caged yellow perch (*Perca flavescens*) receiving Cd from reference diet + reference water (reference), Cd-contaminated diet + reference water (food only), reference diet + Cd-contaminated water (water only), and Cd-contaminated food + water (food and water). Also shown are Cd concentrations in indigenous yellow perch sampled on days 0, 15, and 30 from Lakes Opasatica (solid bars) and Dufault (open bars). Note the break in the vertical axes. All statistical analyses were carried out on the 30 day data set. Comparisons between indigenous yellow perch from Lakes Dufault and Opasatica are represented by an asterisk (*; $P \leq 0.001$); significant differences in Cd concentrations in caged fish are represented by different letters ($P \leq 0.05$). On day 30, $N = 1$ (# symbol) for the reference fish.



tions were not significantly higher in perch exposed only to diet-borne Cd compared with Lake Opasatica perch (Student's *t* test; $P > 0.05$). Furthermore, for perch exposed only to aqueous metal, Cd concentrations in these two organs were not significantly different than those measured in perch exposed to Cd to both aqueous and dietary Cd (Figs. 1*b*, 2*b*). By the end of the exposure period, Cd concentrations in the gills and kidney of caged fish exposed to aqueous Cd either alone or with the Cd-contaminated diet were still significantly lower than those measured in indigenous Lake Dufault perch (Student's *t* test; $P \leq 0.001$).

Subcellular Cd partitioning within the liver

For comparison purposes, we determined Cd subcellular partitioning not only in the livers of caged fish but also in perch living naturally in the two study lakes (Table 3). In indigenous fish from the reference lake, Cd concentrations were slightly higher in the HSP fraction than in other sub-

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Table 3. Mean cadmium concentrations [Cd] (± standard error; $N = 3$ composites of two–five livers) in the various subcellular fractions of indigenous Lake Opasatica yellow perch (IND-OP, *Perca flavescens*) and indigenous Lake Dufault yellow perch (IND-DU) sampled on day 30 of the study.

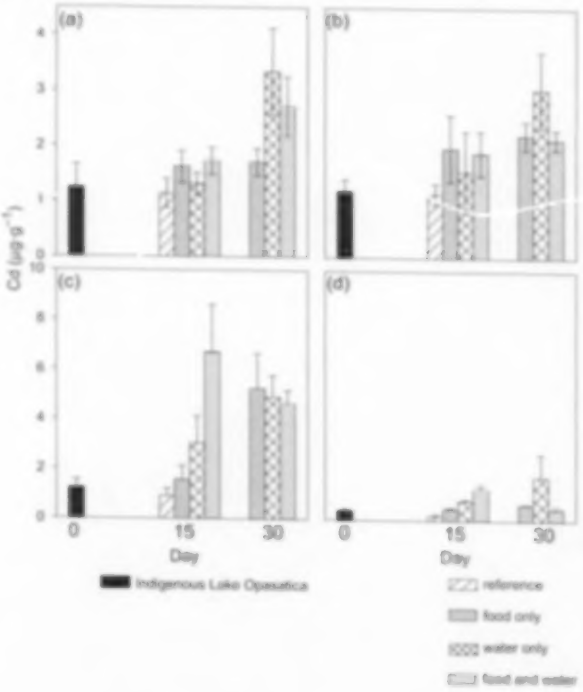
	[Cd] (μg·g^{-1} dry weight liver)			
Sample	Cellular debris	Organelles	HDP	HSP
IND-OP	0.61±0.08ab	0.78±0.09ab	0.43±0.05a	1.24±0.29b
IND-DU	3.69±0.66a	3.70±0.81a	1.80±0.09a	9.18±0.78b

Note: Differences in [Cd] among fractions were compared with a one-way analysis of variance ($P \leq 0.05$). Means followed by the same letter within each lake are not significantly different ($P \leq 0.05$; Tukey–Kramer honestly significant difference post hoc test). HDP, heat-denaturable proteins; HSP, heat-stable proteins.

cellular fractions. This difference was more marked in perch from Lake Dufault, where Cd concentrations in the HSP fraction were about two times higher than those in the other subcellular fractions. On the other hand, within a given lake, hepatic Cd concentrations in the remaining fractions (organelles, HDP, and cellular debris) did not differ significantly (Table 3). During the diet manipulation study, there was no clear effect of Cd source on Cd subcellular concentrations nor on their relative distribution after 30 days of exposure. Mean Cd concentrations increased ~3-fold in the HDP fraction in fish exposed to aqueous Cd only (WO) from day 0 to day 30. Similar increases were observed in perch receiving dietary plus aqueous Cd (Fig. 3*a*). In the organelle fraction, Cd concentrations increased about two to three times (Fig. 3*b*) between days 0 and 30 for all fish receiving Cd, but because of variability in the data, none of these increases were significant ($P > 0.05$). In the heat-stable protein fraction, however, dramatic increases in Cd concentrations were observed; concentrations in this fraction on day 30 were approximately five times higher than initial values for all fish receiving Cd (Fig. 3*c*).

To better interpret the trends in the various subcellular fractions, we considered the quantity of Cd in three metal pools in the caged fish: a detoxified metal pool (HSP), including heat-stable proteins such as metallothionein; a metal-sensitive fraction (MSF) composed of organelles and HDP; and a pool containing cellular debris. At time 0, the cellular Cd burden was low and the majority (~60%) was associated with the MSF, compared with ~30% of the cellular Cd burden associated with the HSP pool. After 30 days of exposure to Cd, the proportion of Cd associated with the HSP fraction had increased from 30% at time 0 to approximately 50%, 40%, and 46% for fish exposed to food only, water only, and food and water, respectively; concurrently, the respective proportions of Cd associated with the MSF had decreased from 60% at time 0 to approximately 40%, 48%, and 48% (Fig. 4).

Fig. 3. Temporal changes in cadmium (Cd) concentrations in hepatic subcellular fractions containing heat-denaturable proteins (*a*), organelles (*b*), heat-stable proteins (*c*), and cellular debris (*d*) in yellow perch (*Perca flavescens*) receiving Cd from reference diet + reference water (reference), Cd-contaminated diet + reference water (food only), reference diet + Cd-contaminated water (water only), and Cd-contaminated food + water (food and water). Also shown are Cd concentrations in subcellular fractions of fish sampled at time 0 (Lake Opasatica yellow perch; solid bars). Reference fish on day 30 were omitted because only one fish was recovered on this day.



Discussion

Metal accumulation at the organ level

In our study, only aqueous Cd influenced branchial Cd concentrations in caged perch. Since the gills are constantly being irrigated with water for respiration and to maintain acid–base balance and ionoregulation, this result is not surprising. Branchial accumulation occurs rapidly when fish are exposed to elevated aqueous levels of this metal (McGeer et al. 2000; De Smet et al. 2001). This is in agreement with Kraal et al. (1995), who noticed a similar increase in branchial Cd in response to aqueous, but not dietary, Cd in a previous laboratory study on the common carp (*Cyprinus carpio carpio*).

The lack of an increase in branchial Cd concentrations between 15 and 30 days in caged fish exposed to aqueous Cd

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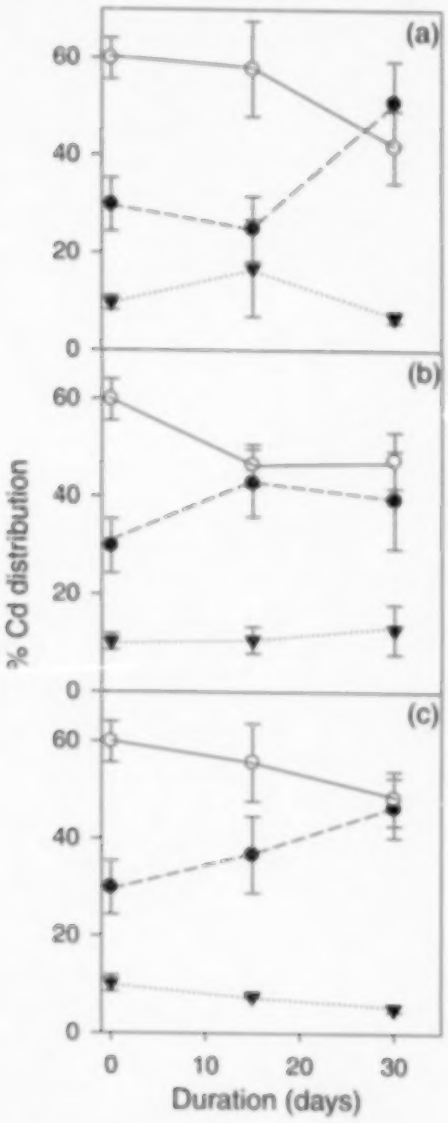
Fig. 4. Temporal changes in the amount of cadmium (Cd) present in detoxified fractions (heat-stable proteins; solid circles), potentially metal-sensitive fractions (open circles), and cellular debris (solid triangles), expressed as a percentage of total cellular Cd in yellow perch (*Perca flavescens*) receiving Cd-contaminated food only (*a*), Cd-contaminated water only (*b*), and Cd-contaminated food + water (*c*).



(either alone or with Cd-contaminated food) suggests that steady state had likely been reached in this organ. However, if steady state had been reached, Cd concentrations in these two treatment groups should have been statistically similar to indigenous Lake Dufault perch, which was not the case, as branchial Cd concentrations were still significantly lower ($P \leq 0.001$) in the caged fish compared with indigenous Lake Dufault perch at the end of the study. Having been chronically exposed to Cd over their lifetime, Lake Dufault perch may have developed mechanisms for coping with excess Cd, such as storage in detoxified forms, resulting in higher steady-state concentrations of this metal in their gills.

A similar dominant influence of aqueous Cd was observed for the kidneys. The relative unimportance of dietary Cd for renal accumulation observed in this study is supported by results from a previous field transplantation study where juvenile perch were transplanted from Lake Opasatica to Lake Dufault to monitor Cd accumulation dynamics (Kraemer et al. 2005). In that study, fish were exposed to the same aqueous levels as those in the current study, but perch were allowed to feed to satiation on the indigenous zooplankton, whereas the current study used a ration of 10% body weight·day^{-1}. After 30 days of exposure, renal Cd concentrations in the latter study (12.7 ± 0.9 μg·g^{-1}) were not statistically different ($P > 0.05$; *t* test) from renal concentrations in perch exposed to Cd-contaminated food and water (12.3 ± 1.3 μg·g^{-1}) or aqueous Cd only (9.8 ± 1.0 μg·g^{-1}) in the current study. In other words, these independent studies demonstrated similar renal Cd concentrations after the same exposure time, regardless of the ration quantity. The dominance of the aqueous route for renal Cd accumulation can be explained by the physiological roles and circulatory position of the kidney within the fish. Located dorsally, the kidney in freshwater fish is supplied by both arterial and venous blood (Larsen and Perkins 2001). Freshwater fish produce a large amount of urine, and a high cardiac output of oxygenated blood from the gills via the arterial system is required to produce enough pressure in the glomeruli to drive the filtration process; this high blood flow exposes the kidney to waterborne contaminants that have been taken up via the gills.

Cd concentrations in the gut were also strongly affected by aqueous Cd, but less so by dietary Cd. This result is somewhat surprising, since freshwater fish drink little water and accumulation in the gut might normally be assumed to result from dietary uptake. However, the gut may also have a role in metal depuration, and increases in gut Cd concentrations seen in fish exposed only to aqueous Cd could reflect elimination via biliary excretion into the gut, followed by some retention of the excreted Cd in the intestinal mucous layer. It has been shown that renal excretion of Cd in fish is low, indirectly lending support to the hypothesis that biliary excretion may play an important role in Cd elimination (Giles 1988). Another possibility is that the gut is simply able to store Cd taken up by the gills. Gut Cd concentrations in caged perch exposed to aqueous Cd (either alone or with dietary Cd) were not significantly different from those in indigenous Dufault fish ($P > 0.05$), suggesting that steady state had been reached. Unlike the situation with the gills, there appears to be no difference in how the Lake Opasatica and Lake Dufault perch populations accumulate Cd in this organ when exposed to the same contaminated environment.

Similar to the gut, the liver was also influenced by both aqueous and dietary Cd, showing increases in hepatic Cd after 30 days in perch exposed to Cd, independent of the exposure route. The liver has a role in maintaining homeostasis by processing and redistributing nutrients taken up during digestion. Thus, the shared importance of both dietary and aqueous routes for hepatic Cd is likely related to the unique location of the liver receiving not only oxygenated blood

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from the dorsal aorta via the hepatic artery, but also venous drainage from the gut via the hepatic portal vein (Hinton et al. 2001). Note, however, that Cd accumulation in the liver after 30 days was not strictly additive (i.e., hepatic Cd burdens in the waterborne + diet-borne treatment (FW) were less than the sum of the burdens in the food-only (FO) + water-only (WO) treatments). We speculate that Cd uptake via the gills can affect uptake from the gut (negative feedback) or vice versa (Kamunde et al. 2002). Alternatively, biliary excretion may be initiated when liver Cd concentrations exceed a certain threshold, thus reducing accumulation below the level expected on the basis of strict additivity.

Hepatic subcellular partitioning of Cd

Long-term aqueous and dietary exposures to metals have been reported to cause negative effects, including reductions in growth and survival (Woodward et al. 1995), physiological impairment (Laflamme et al. 2000; Levesque et al. 2002), and increased lipid peroxidation (Farag et al. 1994). Therefore, we anticipated that the examination of changes in the subcellular partitioning of Cd in response to aqueous and dietary exposure would lead to a better understanding of the mechanisms of metal toxicity and detoxification that underlie these effects seen at the organism level.

The importance of the HSP fraction in Cd accumulation was most evident in indigenous Lake Dufault fish. Cd concentrations in this subcellular fraction were about two times higher than those in the other fractions. The HSP fraction contains a variety of cellular ligands, including amino acids, low molecular weight peptides such as glutathione, and metallothionein. Among these ligands, metallothionein is of particular interest, as this sulphur-rich protein readily binds soft, class B metals such as Cd (Mason and Jenkins 1995). The importance of this protein in the sequestration of cellular Cd has been well documented in fish (Olsson and Hogstrand 1987; Laflamme et al. 2000; De Smet et al. 2001). Unlike indigenous Lake Dufault perch, Lake Opasatica perch (low hepatic Cd concentrations) had Cd concentrations that were more or less evenly distributed among all the subcellular fractions, including the HSP fraction. Furthermore, when compared on a compartmental basis, the majority of the Cd burden was associated with the potentially metal-sensitive fractions (containing organelles and HDP). As hepatic Cd concentrations were low in these reference fish, these results were likely due to low metallothionein production within the liver, resulting in a more or less even distribution of Cd among physiologically sensitive and detoxified cellular components. The subcellular partitioning of Cd in the caged fish represented a transition between the two distribution patterns seen in the indigenous perch populations. For example, when total hepatic Cd concentrations were still relatively low (e.g., Cd-contaminated food only, 15 days), the subcellular distribution of Cd mimicked that seen in indigenous Lake Opasatica fish. When total hepatic Cd concentrations increased (e.g., food and water exposure, 30 days), the subcellular distribution changed, becoming more similar to the distribution seen in indigenous Lake Dufault perch.

To determine if Cd was accumulating differently in fish exposed to the various Cd treatments, we examined changes in Cd accumulation within the HSP fraction and the metal-sensitive fractions. Here the general trend was an increase in the percentage of Cd associated with the HSP fraction and a decrease in Cd associated with metal-sensitive fractions as time progressed, regardless of the exposure route. To determine if this accumulation was linked to differences in potential toxicological impact, we examined changes in Cd concentrations in the subcellular fractions. Concentrations here increased most dramatically in the HSP fraction, in all fish receiving Cd, regardless of the exposure route. In the HDP fraction (i.e., a metal-sensitive fraction), Cd concentrations had increased approximately 3-fold by day 30 in fish receiving Cd via aqueous routes (either alone or with dietary Cd). In contrast, Cd concentrations in the HDP fraction increased by a factor of only ~1.5 in fish receiving Cd from dietary sources only. These results indicate that metallothionein is induced in response to Cd exposure, regardless of the exposure route. When fish were exposed to aqueous Cd (either alone or with dietary Cd), total hepatic Cd accumulation was much higher than that for the food-only exposures and metal detoxification was less effective (i.e., at the subcellular level there was appreciable accumulation in metal-sensitive fractions (HDP)).

In conclusion, we have demonstrated experimentally in the field that Cd accumulation in juvenile yellow perch is dependent on both aqueous and dietary sources, depending on the organ studied. Whereas only aqueous Cd appeared to be important for gill and kidney Cd accumulation, both dietary and aqueous Cd influenced the gut and liver. Changes in hepatic subcellular partitioning during the various treatments showed that Cd handling was similar in all exposure regimes, that is, it was insensitive to the route of exposure. The importance of metallothionein induction as a mechanism of sequestering and thus detoxifying cellular Cd was reinforced in this study. However, when the rate of Cd accumulation was high (i.e., in the aqueous exposures), metal detoxification was less effective. The results of this study suggest that both diet-borne and waterborne Cd play a role in Cd accumulation and thus should both be factored into predictive models for metal-impacted ecosystems.

Acknowledgements

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Characterizing north temperate lake littoral fish assemblages: a comparison between distance sampling and minnow traps

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Abstract: To determine which sampling method may be best employed to monitor changes in fish species composition in littoral areas of small north temperate lakes (≤50 ha), data were collected using distance sampling, based on the line transect method, and a traditional fish sampling method of baited minnow traps. These methods were independently biased in terms of their estimates of species presence and abundance. However, analyses of fish community structure indicated that minnow trap data alone provided a better measure of community structure than did distance sampling data alone. Distance sampling, although a powerful tool in estimating population density, is hindered by a multitude of environmental variables that do not preclude the use of minnow traps. Lakes with clear water containing few species with abundant individuals are best suited for distance sampling. Minnow traps proved to be a fast, efficacious sampling method capable of fairly accurately defining the littoral small-fish community structure in most lakes sampled. These traps are a reliable method for monitoring presence or absence and relative abundance of small-bodied fish species in north temperate lakes. However, the combination of minnow traps and some form of visual sampling will help to ensure that all species are detected in small north temperate lakes.

Résumé : Afin de déterminer quelle méthode d'échantillonnage convient le mieux pour suivre les changements de composition en espèces des poissons de la zone littorale de petits (≤50 ha) lacs tempérés boréaux, nous avons rassemblé des données selon un échantillonnage des distances, une méthode de transect linéaire et une méthode traditionnelle d'échantillonnage de poissons à l'aide de nasses à ménés munies d'appâts. Ces méthodes comportent toutes des erreurs d'estimation de la présence et de l'abondance des espèces. Cependant, l'analyse de la structure de communauté des poissons indique que les données provenant des nasses à ménés seules fournissent une meilleure mesure de la structure de communauté que les seules données de l'échantillonnage des distances. L'échantillonnage des distances, bien qu'un outil puissant pour l'estimation de densité des populations, est affecté par une multitude de variables environnementales qui n'empêchent cependant pas l'utilisation des nasses à ménés. Les lacs à eau claire contenant un petit nombre d'espèces abondantes conviennent mieux à l'échantillonnage des distances. L'utilisation des nasses à ménés s'est avérée être une méthode rapide et efficace d'échantillonnage qui permet de définir assez précisément la structure de communauté des poissons de petite taille dans la plupart des lacs étudiés; c'est une méthode fiable pour suivre l'évolution de la présence ou l'absence et de l'abondance relative des espèces de poissons à corps de petite taille dans les lacs tempérés boréaux. Cependant, la combinaison de l'utilisation de nasses à ménés et d'une forme quelconque d'échantillonnage visuel permet d'assurer que toutes les espèces sont recensées dans les petits lacs tempérés nordiques.

[Traduit par la Rédaction]

Introduction

Recent studies (McGinn 2002) suggest that global warming has the potential to alter the distribution and influence the rates of extirpation of some fish species in north temperate lakes, in particular small-bodied, littoral species (Jackson and Mandrak 2002). Therefore, it is important to monitor changes in fish community structure within these lakes. Estimates of fish abundance, composition, and distribution are critical components of ecological studies attempting to examine community structure and organization. Choice of collection method influences both presence or absence data and abundance estimates (Connolly 1994), and some studies have attempted to compare fish-collection methods (e.g., Jackson and Harvey 1997). Baited minnow traps have a long history in their use to estimate small fish species populations (e.g., He and Lodge 1990) or whole-lake assemblages (e.g., Bendell and McNichol 1987). Estimates of fish abundance using trapping methods are biased by size selection (Pierce et al. 1994), species selectivity (Holland and Peters 1992), water

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temperature (Stott 1970), use of bait (Gerhardt and Hubert 1989), seasonality, sampling location, and fishing time (Craig and Fletcher 1982; Hamley and Howley 1985). Other methods of sampling littoral fish communities include electrofishing, seine netting, and trawling, which have their own sets of inherit biases (Hayes 1983).

Problems associated with creating accurate and (or) precise estimates of fish populations because of gear selectivity and bias have stimulated fish ecologists to explore visual assessment techniques. Underwater observation of fishes can be a valuable technique to census populations, assess distributions and habitat utilization, and monitor behavior (Griffith 1981). An alternative to using visual enumeration techniques to estimate population density is to use sighting models based on distance sampling (Eberhardt 1968; Burnham and Anderson 1976; but see Buckland et al. 2001 for a thorough introduction to distance sampling, and Buckland et al. 2004 for an advanced look at distance sampling). These methods have been used extensively in wildlife studies (e.g., Gates and Smith 1980; Guthery 1988) and found to provide reliable density estimates despite problems surrounding visual sampling.

Distance sampling employing line transects is based on the probability of detecting groups or individuals depending on their perpendicular distances from a randomly set transect line. Distance sampling techniques are distinguished from other visual-census techniques in that the ability of an observer to detect the target object is expected to decrease with increased distance from the line transect. Distance sampling methods use a detection function that corrects for spatial changes in the observer's ability to detect objects across habitats, unlike other underwater enumeration methods. Density estimates are then calculated based on the rate with which the detectability of the object decreases with increasing distance from the observer. This approach allows for the fact that not all objects will be detected (Buckland et al. 2001), overcoming some of the problems associated with other visual techniques. Studies indicate a preference for distance sampling employing line transects over other visual methods because of greater efficiency and lower variance (Burnham et al. 1985; Thresher and Gunn 1986).

Although line transect methods have been used in wildlife studies for over 40 years, these models based on distances have only been applied sporadically to studies of fish populations (e.g., Thresher and Gunn 1986; Ensign et al. 1995; Kulbicki and Sarramegna 1999), although they have been shown to provide reliable estimates of objects in some lakes (Bergstedt and Anderson 1990). Before accepting distance sampling techniques as being suitable for fish community studies, it is important to know how they compare with other standard fish-collection methods. However, the use of distance sampling has not been compared with traditional fish trapping techniques, such as minnow traps. Given that distance sampling should be best suited for shallow, well-illuminated, littoral sites, we compared these two approaches in the habitat where distance sampling should be at its optimum.

Our study compares the ability of distance sampling, using the line transect method, and minnow traps to detect the presence and quantify the abundance of small-bodied fish in the littoral zone of small, north temperate lakes. We then compare the fish community structure as defined by either method with the fish community structure as defined by a combined data set of both methods.

Table 1. Codes for lakes and lake information, including latitude, longitude, and surface area.

Lake	Abbreviation	Latitude (°N), longitude (°W)	Area (ha)
Bluff	BL	45°35′, 78°20′	8.0
Grindstone	GR	45°11′, 78°52′	32.4
Heron	HE	45°27′, 78°49′	24.0
Jake	JK	45°34′, 78°33′	6.0
Kearney	KE	45°35′, 78°27′	32.0
Little Wren	LWR	45°11′, 78°51′	15.8
Louie	LO	45°23′, 78°44′	30.5
Marmot	MR	45°41′, 78°24′	3.0
Plastic	PL	45°11′, 78°50′	32.6
Poorhouse	PRH	45°22′, 78°45′	30.2
Scott	SC	45°29′, 78°43′	28.0
Sproule	SP	45°36′, 78°23′	43.0
Sunday	SU	45°36′, 78°21′	46.0
Wren	WR	45°11′, 78°42′	49.8

Materials and methods

Study design

We conducted a survey of 14 lakes for fish presence and abundance in mid-July to mid-August 1998 (Tables 1 and 2). Lakes chosen for this study were all ≤50 ha in size and were accessible via hiking, portaging, and canoeing. Secluded lakes were preferred to prevent tampering with sampling gear and other sources of disturbance. Water clarity was an important factor in the selection of sample lakes to allow for the identification of fish under water. Owing to the heterogeneity of lakes chosen and a need to compare habitat complexity types for a joint study (MacRae and Jackson 2001), sampling sites were stratified to include both complex (relatively high quantities of large and coarse woody debris and (or) vegetation) and simple habitats (relative little structure composed mainly of soft bottom). However, all results presented herein are representative of the lake by combining all samples in a given lake. Within each sampling site, distance sampling and minnow traps were randomly sampled within the habitat types, resulting in a stratified, randomized design.

Sampling protocol

The line transect method of distance sampling (hereafter referred to as distance sampling) was employed to identify species composition and to estimate the density of littoral zone fish assemblages. All transects were 5 m in length and were made of nylon rope and small lead weights. A 5 m transect was chosen after a pilot study demonstrated no difference in density estimates and because the coefficients of variation differed little among 5, 10, and 20 m transects. All transects were set parallel to the shoreline, between 1.5 and 3.0 m from shore. As the littoral zone may rapidly increase in depth in some locations, the use of transects perpendicular to shore would have resulted in many transects having one end so deep as to impair the counting and identification of the fish. Therefore, the detection function would change

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Table 2. Codes for species with their common and scientific name.

Common species name	Abbreviation	Scientific species name
Blacknose shiner	BNS	*Notropis heterolepis*
Bluntnose minnow	BNM	*Pimephales notatus*
Brook stickleback	BRS	*Culaea inconstans*
Brown bullhead	BBH	*Ameiurus nebulosus*
Burbot	BU	*Lota lota*
Common shiner	CS	*Luxilus cornutus*
Creek chub	CC	*Semotilus atromaculatus*
Golden shiner	GS	*Notemigonus crysoleucas*
Iowa darter	ID	*Etheostoma exile*
Fathead minnow	FHM	*Pimephales promelas*
Largemouth bass	LMB	*Micropterus salmoides*
Pearl dace	PD	*Margariscus margarita*
Northern redbelly dace – finescale dace	PH	*Phoxinus eos – Phoxinus neogaeus*
Pumpkinseed	PS	*Lepomis gibbosus*
Rock bass	RB	*Ambloplites rupestris*
Smallmouth bass	SMB	*Micropterus dolomieu*
White sucker	WS	*Catostomus commersonii*
Yellow perch	YP	*Perca flavescens*

considerably along each transect. For this reason and to maintain more comparable habitat uniformity within a transect (this also varies with depth), transects were oriented parallel to the shoreline. The water depth and clarity dictated the allowable distance that transects were set out from shore. A total of 90 transects were swum per lake. The only exception was where the lake was too small to allow for this. In these lakes, the entire lake perimeter was swum. Two observers were employed to maximize the number of lakes sampled during the available time. During the previously mentioned pilot study, two observers collected fish and learned how to identify fish (Scott and Crossman 1973) and then spent time learning how to identify these same fish under water. At the end of the pilot study, the observers were tested for fish identification and density estimates between observers were examined. Estimates varied little by species in a given lake, but variation increased as species abundance decreased. This was expected because with fewer observations, the distance sampling method is less precise (Buckland et al. 2001). Prior to sampling, an acclimation time of a few minutes was allowed to reduce disturbance of fish. Observers snorkeled the littoral zone facing the shoreline and identified each fish or group of fish to species and then measured the perpendicular distance of fish(es) from the transect line using a meter stick. Data were immediately communicated (via snorkel) to an assistant who recorded data. Swimming speed was slow and deliberate to prevent disturbance of fish (Eberhardt 1968).

Upon completion of distance sampling, each lake was sampled with minnow traps to identify species composition and estimate the relative abundance of small-bodied fish in the littoral zone fish assemblage. Minnow traps were chosen because they are common gear employed to sample littoral fish assemblages in north temperate lakes (e.g., Bendell and McNichol 1987; Jackson and Harvey 1997), and because they could be set in almost any lake or habitat type. A total of 18 baited minnow traps were set per lake (three per site with a total of six sites per lake). These were commercially available Gee minnow traps with an opening diameter of 2–3 cm and a mesh size of 0.5 cm. Traps were baited with a dry, cereal-based dog kibble and were set near the shoreline at depths ranging from 0.5 to 2.0 m. Traps were set overnight and collected in the morning, with a total fishing time of approximately 16 h. Fishes collected were counted and identified to species and released in situ.

Data analysis

The program Distance 3.5 (Thomas et al. 1998) was employed to calculate density estimates from line transect data. The concept underlying line transect sampling is that the probability of observing the object of interest is a function of its perpendicular distance from the observer (Buckland et al. 2001). Reliable estimates of density from line transect data require three assumptions to be met (Buckland et al. 2001): (*i*) objects of interest directly on the transect line are never missed; (*ii*) objects of interest are observed at their initial location, prior to any movement in response to the observer; and (*iii*) distances are measured exactly, although bins can be used. When precision is required to facilitate statistical comparisons, a coefficient of variation (CV) of less than 20% is desired (Thresher and Gunn 1986); therefore, density estimates with a CV greater than 20% were considered imprecise.

There are a number of detection functions to choose from when analyzing data in Distance 3.5, and the detection function model chosen can influence the estimates of density. Our approach was to choose a fit for a diverse assemblage of species, whereas other studies often focused on one or few species and choose a model accordingly (e.g., Ratti et al. 1983; Anderson and Southwell 1995; Pelletier and Krebs 1997). Thus, for comparative reasons, a desire to be consistent, as well as for logistical and timing reasons, one model was chosen and the same analysis was done for each species. The uniform polynomial model was chosen using the Akaike's Information Criterion test (Buckland et al. 2001). The data were truncated as suggested by Buckland et al. (2001) using a right truncation at 1.8 m.

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Table 3. List of number of species detected in lakes using line transect method and minnow trap sampling.

Lake	Total no. of species	Species only detected by line transects	Species only detected by minnow trap
Bluff	5		GS
Grindstone	3		
Heron	8	WS, BNS	
Jake	6	BRS	
Kearney	9	WS	GS
Little Wren	9	BNS, BNM, CS, SMB	RB
Louie	6		CC, RB
Marmot	3		
Plastic	4		YP, CC
Poorhouse	8		
Scott	3		
Sproule	9	ID	CS, PH, GS
Sunday	8	CS	BBH, CC, PH
Wren	7	CS, LMB, SMB	GS

Note: Species codes are described in Table 2.

Relative abundance estimates of minnow traps were derived from mean catch per unit effort (CPUE) for each species in each lake sampled. Correspondence analysis (CA) was employed to summarize different types of underlying structures of lake fish assemblages and to determine if patterns in fish assemblage structure were dependant on sampling technique. CA was performed with presence or absence data, mean CPUE, and density estimates to detect qualitative and quantitative differences in assemblage structure.

Procrustes analysis was employed to quantify the differences in CA results that used combined sampling data against distance sampling or trap data alone based on the presence or absence data. For this comparison, the combined data matrix was designated the reference matrix. Procrustes analysis compares a pair of data matrices by using a rotational-fit algorithm that minimizes the sum-of-squared residuals between the two matrices (i.e., m^2 statistic; Gower 1971; Jackson 1995; Peres-Neto and Jackson 2001) or using medians in resistant-fit methods (Siegel and Benson 1982). Residuals were calculated between the original values and the best-fit solution using the resistant-fit method. The resultant m^2 value is a goodness-of-fit statistic that describes the degree of concordance between the two matrices (i.e., how well do the two ordination solutions match?). The m^2 ranges from 0, which indicates a perfect match between the two configurations, to 1, a maximum mismatch value.

Results

Species detection and quantification

The distance sampling and minnow trap methods were independently selective and biased in their detection of the presence of all small-bodied fish species in littoral habitats. We show which species were detected by only one method in any given lake (Table 3). Distance sampling was able to detect the Iowa darter (*Etheostoma exile*) in Sproule Lake, which was not captured in minnow traps in the same lake. Only one Iowa darter was captured using minnow traps during the pilot study in Sproule Lake, even though they were relatively abundant during distance sampling (e.g., an average of 6.5 Iowa darters per shoreline swim in Sproule Lake). Distance sampling also detected the presence of bluntnose minnow (*Pimephales notatus*) (in 1 of 14 lakes), blacknose shiner (*Notropis heterolepis*) (in 2 of 14 lakes) and brook stickleback (*Culaea inconstans*) (in 1 of 14 lakes), whereas minnow traps in those same lakes missed them. These (Jake and Little Wren lakes) were lakes that contained few small-bodied species and were dominated by smallmouth bass (*Micropterus dolomieu*), which have been shown to alter the abundance and distribution of small-bodied species (MacRae and Jackson 2001). Distance sampling often detected the presence of young, large-bodied individuals, including largemouth bass (*Micropterus salmoides*), smallmouth bass, and white sucker (*Catostomus commersonii*) (at least one of these species was detected with distance sampling in 4 of the 14 lakes, whereas they went undetected by minnow traps). *Phoxinus* spp. were not detected using distance sampling in lakes where they were not one of the most abundant species, but were caught in minnow traps in these lakes (e.g., 29 were caught in Sunday Lake with a mean CPUE = 1.61, whereas none were detected during distance sampling).

Lakes studied were relatively low in species richness and abundance of fish compared with tropical or south temperate lakes. This led to a low number of observations and resulted in highly variable estimates of density using the distance sampling (Appendix A). Anderson et al. (1979) recommended a minimum of 40 objects be detected when using the line transect method of distance sampling, but that the location of 60–80 objects of interest is preferable. During this study, it was often difficult to achieve 60–80 observations because of the rarity of some species and schooling behavior of fish (i.e., one group of fish equals one observation). For example, species that were rarely observed, such as the bluntnose minnow in Heron Lake, had a density estimate of 0.19 fish·m^{-2} and a relatively high CV of 63.9%; while using minnow traps, we observed a mean CPUE of 0.39 with a CV of 42.3%. However, species that were more abundant, such as *Phoxinus* spp. in Bluff Lake, provided a large number of observations and a density estimate with a relatively low CV (D = 1.6 fish·m^{-2}, CV = 29.1%, mean

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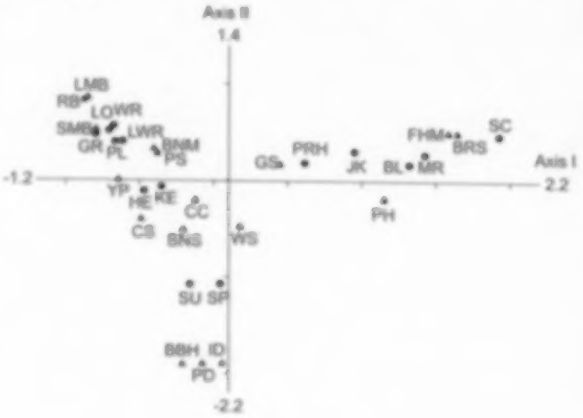
CPUE = 38.0, CV = 17.6%). Burnham et al. (1985) suggested that line transects may avoid and (or) reduce the bias of high variances associated with small sample sizes produced by other distance sampling methods (e.g., strip transect method), because the line transect method adjusts for a decreasing detection function as a function of distance. However, in this study, only those lakes containing few species with abundant individuals were able to produce density estimates with relatively low CVs (Appendix A).

The presence of the observer during distance sampling affected species differently and each species' density estimate differently. One of the assumptions of the distance sampling method is that individuals–groups do not move in response to the observer. Although no response of fish to the observer after the acclimation period was the norm for most species (e.g., blacknose shiner), other species (e.g., rock bass, *Ambloplites rupestris*) were disturbed by the presence of the observer and avoided the sampling area, whereas others appeared to be attracted to the observer (e.g., pumpkinseed, *Lepomis gibbosus*). Clumping did occur at 1 m with many species, which we cannot explain, but it may have been an indication of species avoidance. Species-specific behaviors, such as swimming circles around observers (e.g., common shiner, *Luxilus cornutus*), often made it difficult to ensure that each fish or group of fish was counted only once on a single transect. These results indicate that the mobility and behavior of many species may hinder the use of distance sampling.

The presence of most small-bodied fish species can be detected in a lake 50 ha in size or less when using 15–20 minnow traps (Jackson and Harvey 1997). Therefore, by setting 18 minnow traps per lake, we expected to capture most small-bodied fish species found in the littoral zone. Minnow traps were consistently better than distance sampling at detecting the presence of creek chub (*Semotilus atromaculatus*), golden shiner (*Notemigonus crysoleucas*), *Phoxinus* spp., and rock bass. At least one of these species, and a maximum of three, went undetected by distance sampling in 9 of the 14 lakes. Both methods equally detected the presence of the common shiner, fathead minnow (*Pimephales promelas*), pearl dace (*Margariscus margarita*), pumpkinseed, and yellow perch (*Perca flavescens*). These species were common and relatively abundant in most lakes sampled, with the exception of pearl dace, which was found only in 2 of the 14 lakes sampled. During this survey, brown bullhead (*Ameiurus nebulosus*) were detected in only one lake using minnow traps, while going undetected using distance sampling. Additional sampling in other lakes from the area indicated that brown bullhead were consistently missed by distance sampling but were detected using minnow traps (MacRae 1999).

Species behavior, size, and piscivory may have influenced catches, but the minnow trap method successfully detected the presence of the majority of the small-bodied fish species as compared with a data set of both sampling methods combined. No specific species avoidance behaviors were detected. Given the small body size of littoral species, including juveniles of large species, size selectivity was not an issue (see MacRae and Jackson 2001). The largest fish captured in a minnow trap was a brown bullhead measuring 164 mm, well above the average size of most littoral fish species found in such north temperate lakes in Canada (Scott and Crossman 1973). Size selection of species by minnow traps excluded adults of large-bodied species such as adult white suckers, smallmouth bass, and largemouth bass, and there were times when minnow traps did not detect the juveniles of these species that were observed during distance sampling. However, it is unlikely that this was due to size limitations because small juvenile smallmouth bass, largemouth bass, and white sucker were observed in the littoral zone of these lakes. Thus, it may have been simply gear avoidance.

Fig. 1. Axes one and two from a correspondence analysis using species presence or absence based on combined sampling data. Circles identify lakes, whereas triangles identify species. Abbreviations for lakes can be found in Table 1; species can be found in Table 2.



Species–lake relationships

In this paper, we focus mainly on the comparison of methodologies rather than explaining ecological processes (see MacRae and Jackson 2001); however, it is important to show that different methodologies often alter interpretations of community structure. As indicated earlier, minnow traps and distance sampling have their own inherent biases. Use of only one technique may result in the loss of important data and a biased interpretation of community structure. Therefore we wanted to summarize the fish–lake community structure employing CA using combined sampling data (i.e., the best estimate of community composition) and then compare it to parallel analyses employing distance sampling or trap data alone. Combined presence or absence data from both the minnow traps and distance sampling data represent the most complete presence or absence data set for lakes sampled. The CA using combined sampling data (Fig. 1) during this survey shows a distinct separation of lakes, where lakes composed predominantly of larger, mainly centrarchid species are separated from lakes containing small-bodied species, predominantly cyprinids and the brook stickleback (Fig. 1). Sproule Lake and Sunday Lake are separated from other lakes along the first and second axis by the presence of more rare species (e.g., brown bullhead, Iowa darter, and pearl dace).

Species closest to the origin (i.e., blacknose shiner, common shiner, creek chub, pumpkinseed, and yellow perch) are common species and were found in most lakes. Species positioned at the far end of axis one (i.e., brook stickleback,

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Fig. 2. Axes one and two from a correspondence analysis using species presence or absence data obtained using distance sampling. Circles identify lakes, whereas triangles identify species. Abbreviations for lakes can be found in Table 1; species can be found in Table 2.

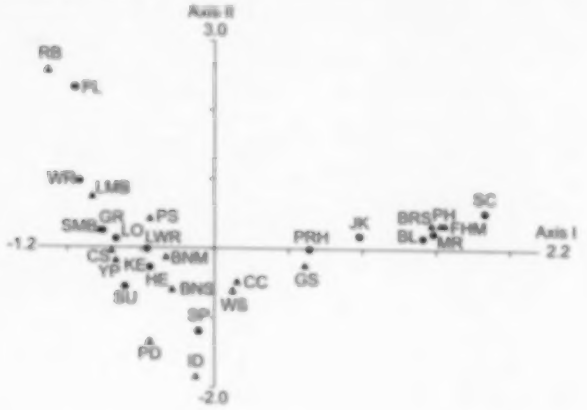
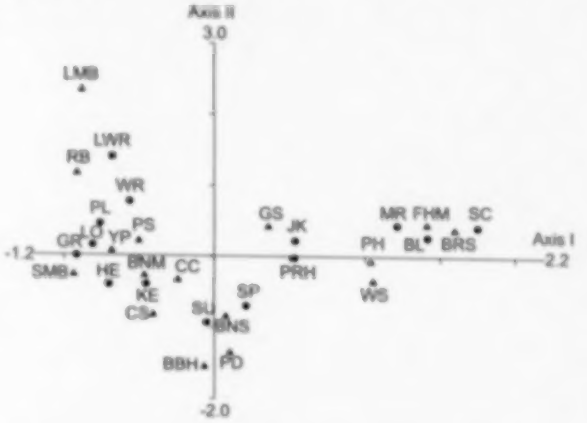


Fig. 3. Axes one and two from a correspondence analysis using species presence or absence data obtained using minnow traps. Circles identify lakes, whereas triangles identify species. Abbreviations for lakes can be found in Table 1; species can be found in Table 2.



fathead minnow and *Phoxinus* spp.) indicate that these species were generally found in the same lakes (Fig. 1). This particular group is separated from the group containing largemouth bass, smallmouth bass, and rock bass, indicating that these two groups were not often found together in the same lake. Blacknose shiner and bluntnose minnow (small-bodied species) are positioned between lakes with and without large-bodied centrarchids.

When we compare the CA of the combined data set (Fig. 1) to the CA of the distance sampling data alone (Fig. 2), the same separation between lakes with and without large-bodied centrarchids is not apparent. Sproule Lake and Sunday Lake appear to be more similar to lakes containing centrarchids because of species undetected by distance sampling. *Phoxinus* spp. were missed using distance sampling alone in both lakes, whereas common shiner and golden shiner were missed in Sproule Lake and creek chub were missed in Sunday Lake.

The CA of the minnow trap data alone (Fig. 3) provides similar trends in underlying data structure in species–lake relationships as the CA based on the combined sampling data (Fig. 1). The second axis is not as clearly separated as the CA based on the combined data set because of the lack of Iowa darter in minnow trap catch data. But overall, the community structure defined by the trap data alone appears to be a closer match to the combined data set than structure defined by the distance sampling data alone.

To evaluate this apparent trend, we compared the similarity of the ordination plots using Procrustes analysis (Peres-Neto and Jackson 2001). The superimposition plot of the lake ordinations (the CA of presence or absence data of combined sampling data and the CA of either distance sampling or minnow trap data alone) shows a strong pattern of concordance for most lakes (Figs. 4*a*, 4*b*). Concordance was stronger for trap data ($m^2 = 0.134$) than for distance sampling data ($m^2 = 0.227$), indicating that the minnow trap data alone provided a summary of the community structure closer to that of the combined data set than did the distance sampling data alone. The largest residuals for the individual lakes based on distance sampling data were Plastic Lake and Sunday Lake. Plastic Lake, an acidic lake, had two of four species undetected by distance sampling, whereas minnow traps detected all four species. Species missed included creek chub and yellow perch. Acidic lakes often have a low species richness and low abundance of fish (Harvey 1989), which may explain why these species were not observed during distance sampling. Sunday Lake had three species not observed in distance sampling, including brown bullhead and two cyprinid species: creek chub and *Phoxinus* spp. The lakes with the smallest residuals employing distance sampling include Marmot, Bluff, Jake, and Poorhouse lakes. Fish assemblages in these lakes consisted of few cyprinid species with abundant individuals, indicating that such lakes would likely be accurately evaluated for presence or absence using distance sampling alone.

The parallel superimposition plot of the species from these lakes for ordination plots of combined data with either distance sampling or minnow trap data alone shows a similar concordance for minnow trap data (resistant-fit Procrustes $m^2 = 0.231$) compared with distance sampling data ($m^2 = 0.213$), although the distance sampling match slightly better (Figs. 5*a*, 5*b*). The largest residuals are found for rock bass based on distance sampling and for white sucker and largemouth bass based on minnow trap data. Rock bass tended to actively avoid the observers and were rarely seen during distance sampling. Both adult and juvenile white suckers were observed during distance sampling, whereas few white sucker juveniles were caught in minnow traps. As well, white sucker adults and adult centrarchids were not captured in minnow traps because of large body size. Largemouth bass were found in only two lakes, Wren Lake and Little Wren Lake, which are connected by a short watercourse. Therefore, largemouth bass collected in minnow traps in Little Wren Lake yet not collected in Wren Lake contributed to the large residual. Only young of the year were found in both lakes. The lowest residuals from the Procrustes analysis were composed mainly of cyprinids (e.g., blacknose shiner, bluntnose minnow, fathead minnow, and golden shiner, as

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Fig. 4. Line segments are residuals between rotated best-fit combined data set and (*a*) distance sampling data only (r^2 = 0.227) or (*b*) trap data only (r^2 = 0.134) for lakes. The line segments connect a point representing a reference position of lakes using combined data to a point representing the best-fit matrix for (*a*) distance sampling data or (*b*) trap data.

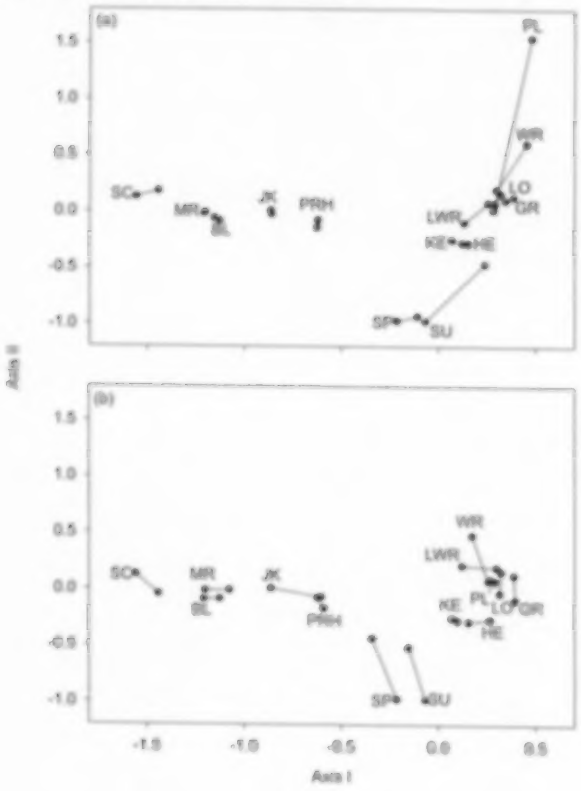
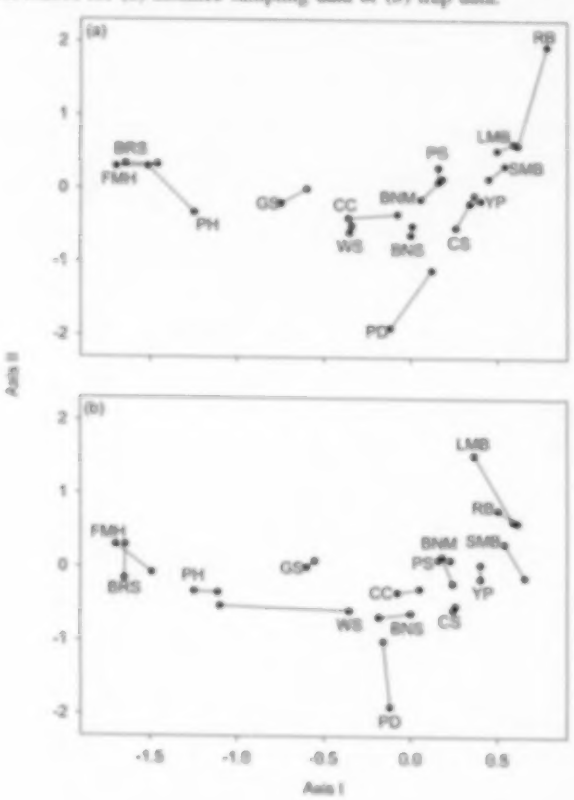


Fig. 5. Line segments are residuals between the rotated best-fit matrix of combined data set and (*a*) distance sampling data only (r^2 = 0.213) or (*b*) trap data only (r^2 = 0.231) for species. The line segments connect a point representing a reference position of species using combined data to a point representing the best-fit matrix for (*a*) distance sampling data or (*b*) trap data.



well as brook stickleback) and the most common species across lakes (e.g., creek chub, common shiner, pumpkinseed, and yellow perch).

The CA based on density estimates from distance sampling resulted in a characteristic arch distortion, which is well documented with CA and other community ordination methods. This resulted in lakes that were most similar in terms of species composition to be found furthest away from each other on the first axis. As well, lakes with dissimilar species compositions were found close together. Owing to this arch effect, we could not easily interpret trends in underlying data structure. Therefore, a comparison between the CA based on mean CPUE and the CA based on density is problematic and has been excluded, although this comparison can be found in MacRae (1999).

Discussion

A recent study by Jackson and Mandrak (2002) predicted that a number of cyprinid species could be threatened with extirpation if global warming leads to the expansion of the distribution of smallmouth bass in Ontario, Canada. Owing to this potential expansion and extirpation of some fish in these north temperate lakes, it is important to monitor these potential changes in fish assemblage structure. To do this, we must determine the most efficacious and accurate sampling methods to monitor these types of changes in species–lake relationships. Our study illustrates that the use of a single method can underestimate species richness and present different ideas of fish assemblage structure in lakes, even when restricted to only the littoral region of each lake. Only with use of multiple gears will most species being targeted be detected (Jackson and Harvey 1997). Both methods examined in this study have inherent biases, but distance sampling was influenced additionally by a number of environmental factors that did not appear to affect minnow traps. Water clarity and general visibility is an important consideration when choosing lakes to employ distance sampling. Several potential lakes were not used in this study because of low visibility, which would have been suitable for sampling with minnow traps or other more standard gears. Substrate often influenced visibility. Lakes with silty bottoms were easily stirred by the transect line and observer, resulting in decreased visibility. Wind also contributed to lack of visibility in those

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lakes with silty bottoms. On very windy days, we were unable to sample because of low visibility caused by suspended materials. Although the models provided by Distance 3.5 (Thomas et al. 1998) can account for low visibility by decreasing the effective strip half-width, fish identification may have been hindered and sample size decreased, leading to estimates of density with high CVs. However, water clarity, substrate, and wind did not appear to hinder the use of minnow traps.

Additionally, the density estimates using distance sampling may have been influenced by species behavior in response to the observer. Such differences in behavior among fish species has been noted and shown to affect estimates for marine fishes (Kulbicki and Sarramegna 1999). Buckland et al. (2001) stated that recording the same animal several times on a single transect can result in a large bias. However, a major underlying problem with distance sampling in north temperate lakes was the lack of observation sizes meeting those recommended by Buckland et al. (2001), thereby resulting in density estimates with high CVs, an indication of possible inaccuracy. Littoral zone fish assemblages of north temperate lakes are more limited in productivity and abundance than tropical and coral reef systems where visual sampling methods are more common, and therefore the need for a large number of observations per species become problems in using distance sampling in north temperate lakes. Reliable estimates of the sighting function can only be obtained with fairly large sample sizes (Ensign et al. 1995), and Anderson et al. (1979) recommended 60–80 observations of groups or individuals. Large amounts of effort in this study resulted in a high number of observations, but of mixed populations. Because individual species density estimates were desired, the observation size obtained was often insufficient to produce a reliable estimate of density (e.g., CV < 20%). Distance sampling may be a more appropriate technique to study highly productive lakes or lakes with few species but highly abundant individuals. Lakes with the greatest clarity and protection from the wind to prevent bottom sediments from stirring up, with firm substrate, and without a steeply sloped littoral zone should be selected for distance sampling. As well, setting line transects perpendicular to shore may ensure that density estimates are not inflated by only recording distances on one side of the transect line (Buckland et al. 2001). However, this has the disadvantage of depth and habitat often changing substantially along the perpendicular transect, thereby leading to a variable detection function along the transect.

Many things can influence the effectiveness of minnow traps, such as size selection (Pierce et al. 1994), species selectivity (Holland and Peters 1992), water temperature (Stott 1970), use of bait (Gerhardt and Hubert 1989), seasonality, sampling location, and fishing time (Craig and Fletcher 1982; Hamley and Howley 1985). Minnow traps used in this study were potentially influenced by all of these variables; however, we view their catches as more representative of the littoral communities, as there was little difference between the fish assemblage structures between the trap data alone and the combined sampling data. Setting numerous traps overnight (16 h) in all habitats types helped to ensure collection of most littoral species. Size selection of fish entering minnow traps was not a concern because cyprinids and other small-bodied littoral species were small enough not to be biased. Minnow traps did not always detect the presence of juveniles of large-bodied species in these lakes, although the juveniles of these larger species should be able to enter the minnow traps.

Minnow traps left in situ overnight have the added benefit of sampling during the crepuscular period. Cyprinid species have been shown to make diel onshore–offshore migrations (Naud and Magnan 1988). These authors showed that *Phoxinus* spp. found in the littoral zone during daylight hours moved offshore to more open areas at night to feed on zooplankton, returning to the littoral zone by sunrise. The increased foraging potential offshore was offset by the need to take refuge from predation during the day. Traps may therefore catch species that avoid open areas during the day because of predation by catching the fish at their most active time (dusk to dawn) in the open areas. Thus, traps may prove to be a more integrated approach to quantifying abundance over time compared with distance sampling. Distance sampling may produce very different results if surveyed in the day or night, although the use of lights at night may bias results differently.

Owing to time restraints, which come with most studies, it is important to consider which method is more time efficient and which is preferable if the goal is to increase precision. It would be much easier and faster to increase the number of traps employed compared with increasing the number of transects swum. Additionally, a wider array of habitats can be sampled using minnow traps, some of which may not be suitable for distance sampling.

The use of presence or absence data has been recommended for fish community studies rather than relative abundance estimates, which often are unreliable (Jackson and Harvey 1997), as has the use of multiple gears to ensure that all species and habitats in a lake are targeted (Jackson and Harvey 1997). The combination of minnow traps and distance sampling data provided a more complete set of presence or absence data for each lake sampled. The combined sampling data resulted in the strongest evidence of species being structured by the presence of littoral predators (MacRae and Jackson 2001). Comparative studies of north temperate lakes indicate that fish assemblages are structured by a variety of abiotic and biotic factors. Predation is considered a principal biotic factor influencing structure of fish communities in north temperate lakes (Jackson and Harvey 1989; Jackson et al. 1992; Olden and Jackson 2001). It is therefore not surprising that the ordination plots showed a separation of lakes with and without large centrarchid species. By comparing the ordination plots of the presence or absence data based on the combined data set with those employing only one sampling method, we found that minnow trap data alone more closely matched the combined data set than did distance sampling alone for the lake data, although they were similar for the species data.

We conclude that when presence or absence data are required to depict species–lake associations of littoral fish communities in north temperate lakes, minnow traps offer an easy and more reliable approach for a greater diversity of habitats and weather than does distance sampling. Minnow

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trap catches, although also variable (Appendix Tables A1 and A2), offer an easily repeatable estimate of relative abundance of most species in north temperate lakes. Therefore, when choosing between minnow traps and distance sampling to determine littoral fish assemblage structure in north temperate lakes, we recommend the use of minnow traps. Ideally, a combination of numerous minnow traps, at least 15–20 per lake, supplemented with other sampling gears to ensure the detection of all life-history stages (Jackson and Harvey 1997) and some form of visual sampling offers the best approach to defining fish assemblage structure.

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Appendix A

Table A1. Mean catch per unit effort of minnow trap data.

	Lake													
Species	BL	GR	HE	JK	KE	LWR	LO	MR	PRH	PL	SC	SP	SU	WR
BNS	0	0	0	0	0.06	0	0	0	0.11	0	0	0.06	0.11	0
BNM	0	0	0.39	0	1.47	0	0.56	0	22.39	0	0	0	0	0
BRS	0.2	0	0	0	0	0	0	0	0.06	0	1.33	0	0	0
BBH	0	0	0	0	0	0	0	0	0	0	0	0	0.06	0
CS	0	0	0.06	0	1.12	0	0	0	0	0	0	0.06	0	0
CC	0	0	2.00	1.44	5.00	0	0.50	0	1.56	0.22	0	2.94	2.50	0
FHM	63.5	0	0	79.06	0	0	0	19.61	53.06	0	51.85	0	0	0
GS	1.3	0	0	5.31	0.18	0.33	0	3.50	0.67	0	0	0.06	0	0.12
ID	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LMB	0	0	0	0	0	0.06	0	0	0	0	0	0	0	0
PD	0	0	0	0	0	0	0	0	0	0	0	0.53	0.06	0
PH	38.0	0	0	45.25	0	0	0	116.83	2.56	0	65.94	0.29	1.61	0
PS	0	12.3	1.39	2.50	0.12	5.83	3.28	0	4.00	5.89	0	0	0.67	4.53
RB	0	0	0	0	0	0.61	1.39	0	0	2.89	0	0	0	0.82
SMB	0	0.2	0.06	0	0.18	0	0.06	0	0	0	0	0	0	0
WS	0.9	0	0	0	0	0	0	0	0	0	0	0.12	0	0
YP	0	0.1	1.50	0	0.24	0.67	0.89	0	0	0.28	0	1.18	0.78	0.06

Note: Abbreviations for lakes can be found in Table 1; species can be found in Table 2.

Table A2. Coefficient of variation for all mean catch per unit effort values for minnow trap data presented in Table A1.

	Lake													
Species	BL	GR	HE	JK	KE	LWR	LO	MR	PRH	PL	SC	SP	SU	WR
BNS					100				103			100	69	
BNM			42		35		62		18					
BRS	58								103		23			
BBH													100	
CS			100		64							100		
CC			37	55	28		69		34	100		22	28	
FHM	15			18				21	41		37			
GS	47			37	73	100		23	103			100		103
ID														
LMB						100								

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Table A2 *(concluded).*

	Lake													
Species	BL	GR	HE	JK	KE	LWR	LO	MR	PRH	PL	SC	SP	SU	WR
PD												37	100	
PH	18			15				11	35		15	100	44	
PS		15	41	27	100	20	29		41	16			34	17
RB						38	23			25				44
SMB		73	100		54		100							
WS	35											68		
YP		100	55		58	54	49			56		24	40	103

Note: Abbreviations for lakes can be found in Table 1; species can be found in Table 2.

Table A3. Density estimates (fish·m^{-2}) for distance sampling data.

	Lake													
Species	BL	GR	HE	JK	KE	LWR	LO	MR	PRH	PL	SC	SP	SU	WR
BNS	0	0	0.04	0	0.27	0.001	0	0	0.15	0	0	0.13	0.19	0
BNM	0	0	0.19	0	0.03	0.006	0.07	0	1.60	0	0	0	0	0
BRS	0.2	0	0	0.03	0	0	0	0	0.00	0	0.31	0	0	0
BBH	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CS	0	0	0.72	0	1.31	0.12	0	0	0	0	0	0	0.01	0.0024
CC	0	0	0.02	0.07	0.065	0	0	0	0.02	0	0	0.0041	0	0
FHM	2.6	0	0	0.79	0	0	0	0.54	3.65	0	7.77	0	0	0
GS	0	0	0	0.022	0	0.14	0	0.31	0.015	0	0	0	0	0
ID	0	0	0	0	0	0	0	0	0	0	0	0.008	0	0
LMB	0	0	0	0	0	0.03	0	0	0	0	0	0	0	0.11
PD	0	0	0	0	0	0	0	0	0	0	0	0.06	0.0012	0
PH	1.6	0	0	0.22	0	0	0	22.64	0.01	0	1.08	0	0	0
PS	0	0.63	0.23	0.05	0.82	0.32	0.08	0	2.12	0.16	0	0	0.02	0.22
RB	0	0	0	0	0	0		0	0	0.003	0	0	0	0.004
SMB	0	0.045	0.13	0	0.08	0.05	0.07	0	0	0	0	0	0	0.16
WS	0	0	0.019	0	0.015	0	0	0	0	0	0	0.019	0	0
YP	0	0.0026	1.47	0	0.35	0.05	0.13	0	0	0	0	0.10	1.10	0.03

Note: Abbreviations for lakes can be found in Table 1; species can be found in Table 2.

Table A4. Coefficient of variation for all density estimates for distance sampling data presented in Table A3.

	Lake													
Species	BL	GR	HE	JK	KE	LWR	LO	MR	PRH	PL	SC	SP	SU	WR
BNS			22		45	76			30			67	63	
BNM			64		40	25	97		14					
BRS	28			12					100		23			
BBH														
CS			60		42	79							114	84
CC			65	45	42				148			45		
FHM	46			37				44	81		12			
GS				77		78		21	101					
ID												41		
LMB						39								110
PD												41	89	
PH	29			37				17	20		18			
PS		62	56	45	43	18	59		68	10			100	8
RB										98				120
SMB		18	32		105	74	100							63
WS			68		108							85		
YP		98	64		42	70	94					30	62	64

Note: Abbreviations for lakes can be found in Table 1; species can be found in Table 2.

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Rapid food web recovery in response to removal of an introduced apex predator

Jesse M. Lepak, Clifford E. Kraft, and Brian C. Weidel

Abstract: Non-native species have increased extinction rates, decreased diversity, altered organism distributions, and constrained ecosystem functioning in native aquatic and terrestrial communities. Although widespread fish introductions have dramatically altered fish communities in north temperate lakes, restoration of native fish communities has been rarely accomplished. This study evaluated a native fish community restoration using a stable isotope based metric. Stable isotopes from a native apex predator (lake trout (*Salvelinus namaycush*)) were used to measure food web changes following removal of a dominant non-native apex predator (smallmouth bass (*Micropterus dolomieu*)). Prior to bass removal, lake trout consumed primarily invertebrates. Within 2 years of the initiation of an experimental removal effort, lake trout $\delta^{13}C$ values (–25.9‰ to –24.9‰) and trophic position (3.5–3.9) increased, reflecting a switch to prey fish consumption that was supported by stomach contents analyses. Here, we show the rapid reestablishment of food web linkages within a native fish community in response to changes in principal energy sources and trophic position of a native apex predator along with the ability to quantify the extent of these changes.

Résumé : Les espèces non indigènes accroissent les taux d'extinction, réduisent la diversité, modifient la répartition des organismes et gênent le fonctionnement des écosystèmes des communautés indigènes aquatiques et terrestres. Bien que les introductions répandues de poissons aient modifié de façon très sérieuse les communautés de poissons des lacs nordiques tempérés, on a rarement réussi à rétablir les peuplements indigènes de poissons. Notre étude évalue la restauration d'un peuplement indigène de poissons à l'aide d'une métrique basée sur les isotopes stables. Les isotopes stables d'un prédateur du sommet du réseau alimentaire (le touladi, *Salvelinus namaycush*) nous servent à mesurer les changements dans le réseau après l'élimination d'un prédateur supérieur dominant non indigène (l'achigan à petite bouche, *Micropterus dolomieu*). Avant le retrait des achigans, les touladis consommaient surtout des invertébrés. En moins de deux ans après le début de l'expérience de retrait expérimental, il y a eu une augmentation des valeurs de $\delta^{13}C$ (–25,9‰ à –24,9‰) et de la position trophique (3,5–3,9) chez le touladi qui reflète un passage à la consommation de poissons comme proies, ce qui est confirmé par les analyses des contenus stomacaux. Nous montrons ici un rétablissement rapide des liens du réseau alimentaire dans un peuplement de poissons indigènes en réaction à des changements des principales sources d'énergie et de la position trophique d'un prédateur supérieur indigène. Nous avons aussi pu évaluer quantitativement l'importance de ces changements.

[Traduit par la Rédaction]

Introduction

Anthropogenic impacts upon north temperate lake ecosystems include broad alterations to lake chemistry (Carpenter et al. 1998; Stoddard et al. 1999) and biotic communities (Whittier and Kincaid 1999). Although methods are available to evaluate water quality restoration within lakes, easily interpretable metrics related to complex energy dynamics have not been used for evaluating restoration of fish communities. Stable isotope analyses have been suggested as a metric to assess fish communities and evaluate the energy dynamics across trophic levels (Vander Zanden et al. 1999, 2003). While stable isotopes have demonstrated the long-term negative impacts of introduced species and the loss of trophic position, no study has yet demonstrated that stable isotopes can also rapidly and effectively document fish community restoration. We implemented a lake manipulation experiment removing a dominant non-native apex predator to test the hypothesis that stable isotope measurements could be used to quantify the restoration of lake food web linkages following reestablishment of a native fish community.

Non-native fishes have decimated native fish communities and reduced the trophic position of native apex fish predators in north temperate lakes (Vander Zanden et al. 1999; Whittier and Kincaid 1999; Jackson 2003). Specifically, smallmouth bass (*Micropterus dolomieu*) are recognized as a primary threat to native fish communities throughout the eastern United States and Canada because they reduce littoral fish abundance and disrupt food web linkages (Chapleau and Findlay 1997; Findlay et al. 2000). Vander Zanden et al. (1999) used stable isotope analyses to demonstrate that bass were capable of displacing native lake trout (*Salvelinus*

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namaycush) as apex predators in a set of lake systems by altering food webs, thereby shortening the food chain length and decreasing mean lake trout trophic position. $\delta^{13}C$ values presented by Vander Zanden et al. (1999) showed that lake trout in lakes where bass were absent were enriched relative to those that had been invaded by bass, indicating a decrease in the amount of littoral prey fish in lake trout diets.

For five decades, non-native smallmouth bass have replaced lake trout as the dominant apex predator and reduced native prey fish abundance in the littoral zone of our study lake, a 271 ha oligotrophic lake (Little Moose Lake, Herkimer County, New York) (Brown et al. 2000; Weidel et al. 2000). Throughout this period of bass dominance, the lake trout population within Little Moose Lake consisted largely of nonpiscivorous lake trout that grew slowly and matured at small sizes (Smith 2000), similar to populations in Ontario lakes described by Martin (1966) and Konkle and Sprules (1986).

An intensive electrofishing effort was initiated and maintained in Little Moose Lake from spring 2000 through fall 2002, resulting in a 90% reduction of adult smallmouth bass (more than 28 000 individuals were removed). Prey fish catch per unit effort increased in spring electrofishing surveys from 2000 to 2002 (greater than twofold increases in abundance were observed for common prey fishes such as brown bullhead (*Ameiurus nebulosus*), pumpkinseed (*Lepomis gibbosus*), and slimy sculpin (*Cottus cognatus*), all of which are consumed by lake trout) (Weidel 2004). Based on these changes in littoral prey fish abundance, we hypothesized a shift in lake trout $\delta^{13}C$ signatures from values indicative of pelagic–profundal energy sources to more littoral values, and we expected lake trout trophic position, as measured by $\delta^{15}N$, to increase owing to increased fish consumption (Vander Zanden and Rasmussen 1999; Post 2002).

Materials and methods

Stable isotope baseline characterization

Following methods in Post (2002), littoral, pelagic, and profundal baselines for $\delta^{13}C$ and $\delta^{15}N$ in Little Moose Lake were established by analyzing a wide range of invertebrates (Diptera, Odonata, Ephemeroptera, Trichoptera, Gastropoda, and Cladocera) and algae collected from May through August 2000–2002. For organisms with a second-order trophic position (i.e., consumers of primary producers), 3.4‰ was subtracted from their measured $\delta^{15}N$ signature to establish a baseline $\delta^{15}N$ value for trophic level 1.

To ensure that sample storage did not influence stable isotope measures, all tested organisms were collected while still alive and then preserved and processed such that fractionation or decomposition did not occur (Post 2002). Two to 50 organisms collected on a given sampling date were homogenized and assayed whenever a single organism did not provide enough material (0.9 mg) for stable isotope analysis. Stable isotopes in prey fish (ranging from 40 to 150 mm and considered consumable by lake trout ranging in length from 264 to 551 mm) were also measured to establish a lake trout isotopic signature that would be expected if they maintained a strictly piscivorous diet.

Lake trout collections and processing

Diet contents were collected and stable isotopes values were measured from 159 lake trout (264–551 mm) collected from April 2000, 1 month prior to initiation of bass removal, through June 2002 by electrofishing, trap netting, and angling.

Gastric lavage was used to collect stomach contents. The procedure was carried out by inserting a soft flexible tube into a lake trout's esophagus and then pumping distilled water into the stomach to expel the contents. This procedure was repeated at least twice for every fish. Lake trout that were thought to still contain stomach contents after manual and visual evaluation were subjected to a third gastric lavage procedure. The effectiveness of this method was evaluated by dissecting approximately 20 fish. In over 90% of these cases, 90% of available stomach contents (by wet weight) were successfully retrieved from the subject fish and minimal residue remained in the stomach.

Lake trout tissue samples were collected from the anterior–dorsal musculature with a biopsy procedure using a 14-gauge, 6 cm needle. Lipids were extracted from all lake trout tissue before analysis (see methods in Folch et al. 1957; Post and Parkinson 2001) to account for the differential routing of stable isotopes in adipose versus muscle tissue (DeNiro and Epstein 1978; Peterson and Fry 1987; Kling et al. 1992).

Littoral carbon estimation

Proportions of littoral and pelagic–profundal energy contributions to lake trout tissue were estimated by comparing $\delta^{13}C$ measurements of lake trout muscle with invertebrate samples. Equation 1 (following Vander Zanden et al. 1999) was used to estimate the relative contribution of littoral energy to lake trout tissue samples, assuming that energy sources were either littoral or pelagic–profundal:

$$(1)\quad \%\ \text{littoral} = \frac{(\delta^{13}C_{\text{lake trout}} - \delta^{13}C_{\text{pelagic–profundal}})}{(\delta^{13}C_{\text{littoral}} - \delta^{13}C_{\text{pelagic–profundal}})} \times 100$$

Diet analysis

Stomach contents were identified and categorized as littoral, pelagic, or profundal as well as fish or non-fish. Stable isotope signatures, life history traits, known distributions, and behavior of organisms were all taken into account when assigning organisms to a lake region (e.g., littoral, pelagic, or profundal). Diet item dry weights were calculated using intact organisms collected from Little Moose Lake of comparable size with those found in lake trout stomachs. Dry weight was estimated by drying organisms for 24–72 h at 60 °C depending on their size.

Lake trout diet data were pooled from every fish sampled in a given year to represent the overall diets throughout the year. These annual diet compilations were used to calculate the relative contribution of littoral, pelagic, and profundal energy sources from 2000 to 2002. Comparison of our results with lake trout dietary data collected from Little Moose Lake during 1996–1997 confirmed that seasonal variation did not greatly influence stomach contents. The 1996 and 1997 diet data encompassed a wider seasonal range (March–December and January–October, respectively) than the

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2000–2002 diet data (April–September, May–December, and January–August, respectively).

Trophic position quantification

A three-source-mixing model, incorporating lake trout diet data, was developed to quantify lake trout trophic position (eq. 2) where TP_{lt} represents lake trout trophic position; α, β, and γ ($\alpha + \beta + \gamma = 1$) represent the proportion of lake trout diets composed of littoral, pelagic, and profundal energy sources, respectively, based on annual stomach content data; and λ is the trophic position of the organisms used for baseline calculation (in this case, trophic position equals 1). A 3.4‰ enrichment of $\delta^{15}N$ was assumed to represent an increase of one trophic position (Vander Zanden and Rasmussen 2001):

$$(2)\quad TP_{lt} = \{[\delta^{15}N_{lt} - (\delta^{15}N_{littoralbaseline} \times \alpha + \delta^{15}N_{pbaseline} \times \beta + \delta^{15}N_{ybaseline} \times \gamma)]/3.4\} + \lambda$$

Stable isotope procedures and statistics

One-way analyses of variance (ANOVAs) and Tukey's pairwise comparisons ($\alpha = 0.05$) were used to test the significance of shifts among years in trout $\delta^{13}C$ signatures and mean trophic position. Source and mixture variability of stable isotope measurements were accounted for using methodology from Phillips and Gregg (2001) and applying the most conservative (95%) confidence interval. Variability of the C:N ratio of major diet items was tested as a possible source of differential fractionation of ^{15}N (Adams and Sterner 2000).

Stable isotope measurements were performed using a Finnigan MAT Delta Plus continuous-flow elemental analyzer at Cornell University's Boyce Thompson Stable Isotope Facility (Ithaca, New York). Samples with high nitrogen content were compared with a methionine standard ($\delta^{13}C$ = –25.40‰, $\delta^{15}N$ = –0.81‰, 40.25% C, 9.39% N) and samples with low nitrogen content were compared with a burned cabbage standard ($\delta^{13}C$ = –27.22‰, $\delta^{15}N$ = 0.77‰, 41.60% C, 3.35% N). The standard error from the mean of each isotopic run never exceeded 0.15‰ with respect to the standards. All statistical analyses were implemented using SPlus (Insightful Corporation, Seattle, Washington). All means are reported with 2 standard errors from the mean (SEM) unless stated otherwise.

Results

Stable isotope baseline characterization

Baseline stable isotope signatures of littoral $\delta^{13}C$ (–20.19‰ ± 0.85‰) and $\delta^{15}N$ (1.64‰ ± 0.75‰) and pelagic $\delta^{13}C$ (–30.15‰ ± 1.39‰) and $\delta^{15}N$ (3.27‰ ± 0.81‰) in Little Moose Lake did not vary significantly during the study (ANOVAs: p = 0.275, F = 1.38, n = 5, 4, 13; p = 0.069, F = 3.44, n = 6, 5, 3; p = 0.677, F = 0.40, n = 4, 4, 8; and p = 0.254, F = 1.5, n = 10, 6, 3 for 2000, 2001, and 2002 littoral and pelagic carbon and littoral and pelagic nitrogen, respectively). Thus, individual measurements of organisms collected in 2000, 2001, and 2002 were pooled to more accurately portray the overall baselines of carbon and nitrogen in the littoral and pelagic zones of Little Moose Lake. Profundal carbon and nitrogen baselines were established for 2002 alone; thus, pooling by year was not necessary.

Baseline pelagic $\delta^{13}C$ (–30.15‰ ± 1.39‰) and profundal $\delta^{13}C$ (–29.22‰ ± 1.30‰) were not distinguishable from each other (ANOVA: p = 0.506, F = 0.46, n = 14, 4 for pelagic and profundal organism signatures, respectively). Thus, pelagic and profundal organism signatures were pooled for comparison of littoral carbon signatures with pelagic and profundal carbon signatures. Littoral zone organisms were enriched in $\delta^{13}C$ (–20.19‰ ± 0.85‰) by comparison with pelagic (–30.15‰ ± 1.39‰) and profundal (–29.22‰ ± 1.30‰) organisms (ANOVA: $p < 0.001$, F = 200.09, n = 22, 18 for littoral and pooled pelagic and profundal organism signatures, respectively; Tukey's pairwise comparison at α = 0.05).

Organisms collected from the littoral, pelagic, and profundal regions were increasingly enriched in $\delta^{15}N$ with respect to sampling location. The pelagic and profundal regions were not found to be significantly different in signature (pelagic = 3.27‰ ± 0.81‰ and profundal = 3.61‰ ± 0.37‰) but were found to be significantly enriched in $\delta^{15}N$ when compared with the littoral zone signature (ANOVA: p = 0.009, F = 5.42, n = 16, 19, 4 for littoral, pelagic, and profundal organism signatures, respectively). A Tukey's pairwise comparison (α = 0.05) confirmed that pelagic and profundal organism signatures were significantly greater than littoral organism values.

Littoral carbon estimation

Lake trout collected for stable isotope and diet analyses (mean length = 444 ± 7.2 mm) did not show a significant size shift during the study period. A significant increase in lake trout $\delta^{13}C$ was observed from 2000 to 2002 (Fig. 1). Source and mixture variability were incorporated into the isotopic model (Phillips and Gregg 2001), and lake trout $\delta^{13}C$ values increased significantly from –25.9‰ to –24.9‰ (±0.36‰ and 0.20‰, respectively) concurrent with smallmouth bass removal (ANOVA: p = 0.032, F = 3.50, n = 16, 50, 93 for 2000, 2001, and 2002, respectively; Tukey's pairwise comparison at α = 0.05).

Diet analysis

No lake trout collected during 2000 contained fish in their stomachs. In 2001, the proportion of fish (by dry weight) in sampled lake trout stomachs increased from 0% to 5%. The proportion of fish (by dry weight) in sampled lake trout stomachs increased dramatically in 2002 to 74% of the total biomass (Fig. 2). Slimy sculpin were the only fish consumed by lake trout during 2001. Lake trout collected during 2002 contained six fish species (brown bullhead, landlocked Atlantic salmon (*Salmo salar*), pumpkinseed, rainbow smelt (*Osmerus mordax*), smallmouth bass, and slimy sculpin) in their diets (Fig. 2).

Following the bass removal, lake trout shifted from a primarily profundal diet (96% and 83% in 2000 and 2001) to a diet composed of 50% littoral inputs in 2002 (Fig. 3). The 2000 and 2001 diets were composed primarily of chironomids. Various species of zooplankton were also abundant in lake trout diets, but they accounted for a negligible proportion of biomass relative to chironomids. Lake trout diets from 1996 and 1997 consisted of more than 70% profundal

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Fig. 1. Points represent lake trout (*Salvelinus namaycush*) $\delta^{13}C$ (‰ ± 2 SEM) by year. Broken horizontal lines represent the expected equilibrium of lake trout with a diet of 100% prey fish, consisting of fish ranging in total length from 40 to 150 mm (–22.08‰), and the most depleted value of $\delta^{13}C$ measured for any lake trout evaluated in this study (–27.97‰). The most enriched $\delta^{13}C$ measured for any lake trout was –22.00‰ and therefore is not shown, as this is nearly identical to the assumed signature of a lake trout with a diet consisting of 100% prey fish.

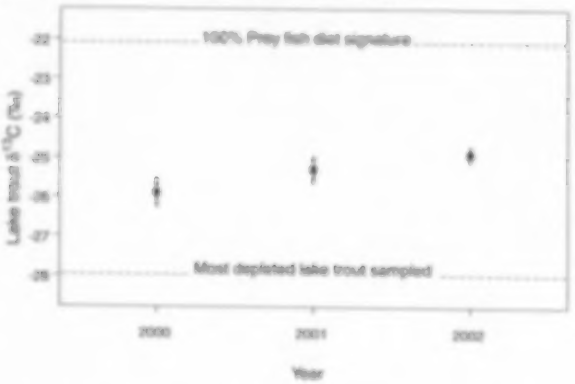
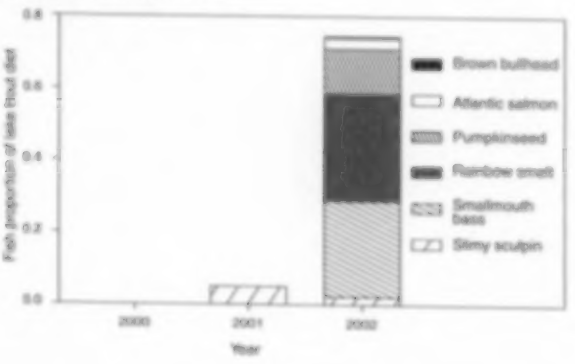


Fig. 2. Annual lake trout (*Salvelinus namaycush*) prey fish diet proportions (by dry weight) from Little Moose Lake. Proportions of brown bullhead (*Ameiurus nebulosus*), Atlantic salmon (*Salmo salar*), pumpkinseed (*Lepomis gibbosus*), rainbow smelt (*Osmerus mordax*), smallmouth bass (*Micropterus dolomieu*), and slimy sculpin (*Cottus cognatus*) consumed are represented by the respective patterns shown.



input, largely chironomids, similar to lake trout in 2000 and 2001. Fish did not comprise a majority of lake trout diet composition until 2002. Stomach fullness (dry weight per individual) for individual lake trout did not vary during the study period (ANOVA: $p = 0.440$, $F = 0.82$, $n = 16, 50, 93$ for 2000, 2001, and 2002, respectively).

Trophic position quantification

The diet-based, three-source-mixing model, using proportions of littoral, pelagic, and profundal inputs to lake trout diets as calculated and displayed in Fig. 3 for 2000, 2001, and 2002, respectively, indicated that lake trout trophic position increased during the smallmouth bass manipulation

Fig. 3. Proportion of lake trout (*Salvelinus namaycush*) diet (by dry weight) made up of prey from littoral (open bars), pelagic (shaded bars), and profundal (solid bars) habitats from Little Moose Lake by year. Numbers within parentheses represent sample size.

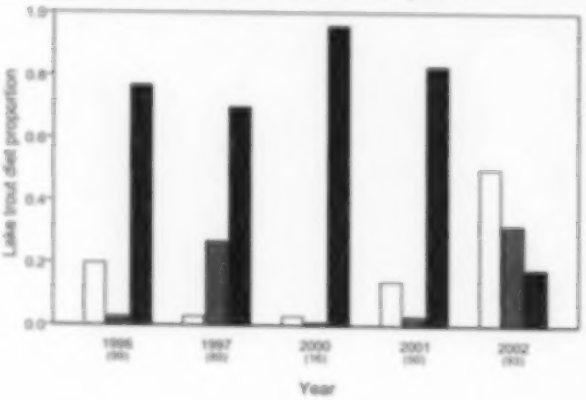
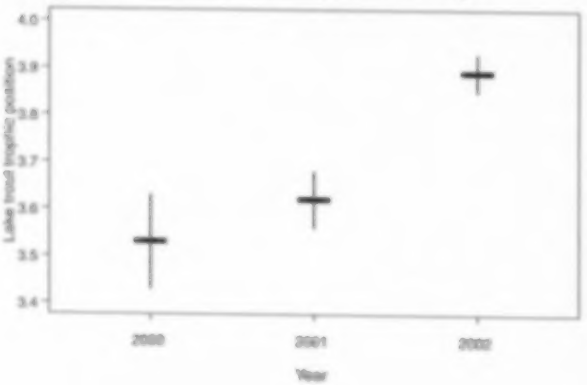


Fig. 4. Annual estimated lake trout (*Salvelinus namaycush*) trophic position (±2 SEM) for each year of the study.



(Fig. 4). The mean lake trout trophic position in 2000 was 3.5 and then increased significantly to 3.6 in 2001 and 3.9 (±0.10, 0.06, and 0.04, respectively) in 2002 (ANOVA: $p < 0.001$, $F = 71.47$, $n = 16, 50, 93$ for 2000, 2001, and 2002, respectively; Tukey's pairwise comparison at $\alpha = 0.05$). The C:N ratio of major diet items ranged from three to five.

Discussion

Lake trout $\delta^{13}C$, diet composition, and associated trophic position responded rapidly to smallmouth bass removal within a 2-year period, reflecting food web linkages characteristic of the native fish community. The observed reestablishment of trophic linkages within a native fish community was unexpected for several reasons. Prior to initiation of this study, it was unknown if and how quickly native prey fish could reestablish abundant littoral populations from available refuges associated with Little Moose Lake, such as tributary streams. It was also unclear whether lake trout could rapidly switch from planktivory to piscivory and utilize newly abundant littoral energy sources. Finally, slow growth rates and corre-

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sponding slow stable isotope turnover rates were expected to limit our ability to identify a lake trout dietary response to food web changes (Hesslein et al. 1993). Despite these limitations, stable isotope measurements identified a rapid response within the lake food web to the removal of a dominant introduced apex predator. Native prey fish responded quickly to this removal and lake trout took advantage of increased prey fish abundance. Stable isotope turnover rates were likely enhanced by increased growth and metabolism resulting from increased consumption of prey fish (MacAvoy et al. 2001; Harvey et al. 2002). Also, the need to use diet data to account for profundal energy sources increased the rate at which trophic position shifts were detectable.

Lake trout diet data closely corresponded to the recovery pattern observed for prey fish within Little Moose Lake. Increases in prey fish abundance occurred in 2001, 1 year after the smallmouth bass removal was initiated (Weidel 2004), and lake trout quickly switched from a primarily profundal (chironomid) diet to one consisting primarily of littoral inputs. Individual stomach fullness did not vary substantially throughout the removal study, suggesting that the increased prey fish in lake trout diets likely resulted from the substitution of prey fish for invertebrates rather than simply consuming more prey fish in addition to the previous invertebrate diet. The increase in littoral prey fish abundance was similar but larger than what has been seen in other studies of predator–prey interactions involving changes in *Micropterus* populations (Carpenter and Kitchell 1993; Mittelbach et al. 1995).

Ecosystem rehabilitation efforts during the past 30 years have generally focused on chemical measures as metrics for lake restoration (Schindler et al. 1996; Stoddard et al. 1999), while analogous measures for evaluating the success of biotic community restoration have not been well developed (Pimm 1991; Lodge 1993). In ecological studies, the use of stable isotopes has provided an improved ability to understand aquatic food web dynamics. With the use of stable isotope analyses and accurate quantification of baseline isotopic signatures, comparisons across a wide variety of aquatic systems are possible (Post 2002).

Metrics such as growth, abundance, and reestablishment of native species are common measures of lake restoration at a population level; stable isotopes provided an enhanced ability to evaluate the reestablishment of trophic linkages involving complicated interactions between habitat use, fish community, and behavior across disparate systems. Vander Zanden et al. (1999) observed a lake trout stable isotope response 6 years after a lake invasion by smallmouth bass, but precise details regarding the timing of this shift were unavailable. Their observed difference in lake trout $\delta^{13}C$ values in bass-invaded versus uninvaded lakes (–29.2‰ versus –27.4‰, difference of 1.8‰; Vander Zanden et al. 1999) was comparable with the changes observed in Little Moose Lake lake trout after 2 years of reduced bass abundance (–25.9‰ versus –24.9‰, difference of 1.0‰) taking into account differences in baseline isotopic values between systems. Also, the mean trophic positions observed by Vander Zanden et al. (1999) for lake trout in lakes where bass were established (3.3) versus lakes where bass were absent (3.9) were similar to those observed in Little Moose Lake during the lake trout trophic shift in response to bass removal (i.e., from 3.5 to 3.9). These values suggest that food web conditions in Little Moose Lake were restored to a condition similar to systems where bass have not been introduced. Stable isotope and diet data allowed us to quantify a food web recovery as well as compare food web condition and energy input within our study lake with those of other north temperate lakes.

Our study documents a rapid food web response to changes in fish community abundance and reinforces the need to integrate diet and isotope data when evaluating shifts in complicated ecosystems (i.e., three or more disparate energy sources). Typical in many lake systems, Little Moose Lake pelagic and profundal $\delta^{13}C$ baseline values were indistinguishable; therefore, it was impossible to use only $\delta^{13}C$ values to differentiate between pelagic and profundal energy sources (Peterson and Fry 1987; Vander Zanden and Rasmussen 1999; Post 2002). Thus, implementation of the three-source-mixing model required establishment of environmental baselines for each energy source incorporated in lake trout diets, and lake trout diet data provided the ability to distinguish between pelagic and profundal invertebrate sources and littoral prey fish (Post 2002).

Two specific concerns could have limited our ability to accurately interpret observed stable isotopic values. First, accurate quantification and assessment of variability in Little Moose Lake isotopic baselines were necessary. The profundal $\delta^{13}C$ and $\delta^{15}N$ baselines in our study were established from samples collected exclusively during 2002. Baseline variation is expected and is likely caused by ambient environmental factors that could have changed during the study (Vander Zanden and Rasmussen 1999). However, the profundal baseline was consistent with previous stable isotope measurements in organisms collected from Little Moose Lake in 1999 (Smith 2000) as well as samples subsequently collected during 2003 (J.M. Lepak, unpublished data). Baseline values derived from littoral and pelagic zone invertebrates corresponded to patterns seen in other research, and the isotopic values of longer-lived Little Moose Lake prey fish were also consistent with those of numerous other studies (Vander Zanden et al. 1999; Post 2002). By incorporating error estimates in our isotopic baseline values (Phillips and Gregg 2001), we were able to include both source and mixture variability in our results. Second, differences in C:N ratios of diet items can affect the fractionation of nitrogen. C:N ratios within lake trout diet items ranged from 3 to 5; therefore, we assumed that differential fractionation of ^{15}N was unlikely to have influenced these results because these C:N values were below the ratio at which this influence would be likely to occur (Adams and Sterner 2000).

Little Moose Lake, similar to many lakes in North America, has been exposed to pervasive anthropogenic changes during the past 50 years. The restoration effort reported in this study is broadly applicable to numerous north temperate lake ecosystems because (*i*) oligotrophic systems dominated by lake trout apex predators were historically common throughout more than 3500 lakes within North America's Northern Hardwood – Boreal transition zone alone (Gunn et al. 2004), (*ii*) the study lake is comparable in size with the majority of these north temperate lakes (Gunn et al. 2004),

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and (*iii*) the Little Moose Lake fish community is similar to that of many other lakes with limited pelagic forage fish in which resident lake trout populations are particularly vulnerable to littoral predator introductions (Vander Zanden et al. 1999).

Smallmouth bass continue to be widely introduced throughout North America, despite well-documented negative impacts (Whittier and Kincaid 1999; Jackson 2003). Although removal of non-native predators has been implemented to restore lake ecosystems, such efforts have generally involved poisoning the entire fish community and then stocking a small number of native species (e.g., one predator and one prey fish; see Harig and Bain 1998). Efforts to evaluate restoration of lake fish communities have implemented complicated metrics of biotic integrity (Harig and Bain 1998) or have estimated the change in consumption by non-native predators based on the number of removed predators (Ruzycki et al. 2003). We present an alternative approach using stable isotope measurements and diet content analyses to evaluate the restoration of food web linkages in a large lake with a diverse fish community. The observed response was rapid, suggesting that it is possible to remove predators to restore native fish communities and use stable isotopes to measure the reestablishment of lake food web linkages within a recovering fish community.

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The Gibbs and split–merge sampler for population mixture analysis from genetic data with incomplete baselines

Jerome Pella and Michele Masuda

Abstract: Although population mixtures often include contributions from novel populations as well as from baseline populations previously sampled, unlabeled mixture individuals can be separated to their sources from genetic data. A Gibbs and split–merge Markov chain Monte Carlo sampler is described for successively partitioning a genetic mixture sample into plausible subsets of individuals from each of the baseline and extra-baseline populations present. The subsets are selected to satisfy the Hardy–Weinberg and linkage equilibrium conditions expected for large, panmictic populations. The number of populations present can be inferred from the distribution for counts of subsets per partition drawn by the sampler. To further summarize the sampler's output, co-assignment probabilities of mixture individuals to the same subsets are computed from the partitions and are used to construct a binary tree of their relatedness. The tree graphically displays the clusters of mixture individuals together with a quantitative measure of the evidence supporting their various separate and common sources. The methodology is applied to several simulated and real data sets to illustrate its use and demonstrate the sampler's superior performance.

Résumé : Bien que les mélanges de populations contiennent des contributions des nouvelles populations en plus de celles des populations originales déjà échantillonnées, les individus non identifiés du mélange peuvent être séparés en fonction de leur source par leurs caractéristiques génétiques. Nous décrivons un échantillonneur de Gibbs de type Monte Carlo avec procédure de séparation–regroupement par chaînes de Markov qui sépare successivement un échantillon contenant un mélange génétique en sous-ensembles plausibles d'individus à la fois de la population d'origine et des populations additionnelles présentes. Les sous-ensembles sont sélectionnés de manière à satisfaire aux exigences de l'équilibre Hardy–Weinberg et de l'équilibre de liaison attendus dans de grandes populations panmictiques. Le nombre de populations présentes peut être estimé à partir de la distribution des nombres de sous-ensembles par partition retirés par l'échantillonneur. Afin de mieux résumer le produit de l'échantillonneur, les probabilités d'attribution conjointe des individus du mélange aux mêmes sous-ensembles sont calculées à partir des partitions et elles servent à construire un arbre binaire de leur degré de parenté. L'arbre représente graphiquement les groupements d'individus du mélange de même qu'une mesure quantitative des données qui appuient leurs différentes sources séparées et communes. Nous appliquons la méthodologie à plusieurs ensembles de données réelles et simulées afin d'en illustrer l'utilisation et de démontrer la performance supérieure de cet échantillonneur.

[Traduit par la Rédaction]

Introduction

Analysis of population mixtures using genetic data has advanced materially since its beginnings in the 1980s. The early development focussed on resolving the source proportions contributed by separately breeding populations that had evolved differences in their genetic makeup. The source composition was to be assessed from a random sample of the multilocus genotypes in the mixture and a so-called baseline composed of independent genetic samples from each of the possible contributing populations. The population origins of the individuals in the baseline samples were assumed known with certainty. The finite mixture model and maximum likelihood estimation were introduced as the foundations for a statistical methodology to solve this source composition estimation problem (Fournier et al. 1984; Millar 1987; Pella and Milner 1987). The continued use of the finite mixture likelihood methodology to the present (e.g., Beacham and Wood 1999; Debevec et al. 2000; Urawa et al. 2003) is a testament to its sound theoretical basis and its favorable history of performance in widespread applications. Recent adoption of the sampling models into a parallel Bayesian estimation method (Pella and Masuda 2001) underscores the merit seen in the original finite mixture construct. However, the requirement by the methodology that baseline samples from the entire set of populations composing the

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mixture be available before estimating the population composition has been an impediment. In many practical applications, the baseline is suspected or known to be incomplete. If the mixture contains extra-baseline individuals, they must be overlooked to apply the method with the hopeful justification that such individuals are presumably few in number or minor in proportion. Furthermore, their contributions likely are assigned by the methodology to baseline populations that are genetically similar to their extra-baseline sources. Such misassignment may be meaningful and acceptable at times, for example, if geographical genetic structure occurs and regional composition is of interest. Nonetheless, ignoring the extra-baseline populations is often unsatisfactory and unreasonable.

Concerns and interest about extra-baseline populations and their contributions to the population mixture motivated Smouse et al. (1990) to accommodate incomplete baselines in the statistical modeling. A general recipe was proposed, related to methods first developed by Makela and Richardson (1977), which included sequential hypothesis testing for the populations present and estimation of their contributions when detected. However, the particular order of tests for presence of the possible subsets of baseline and extra-baseline populations was left unresolved, critical values for the likelihood ratio tests were considered to be only rough approximations, and probable bias in composition estimation related to size and power of tests was not considered. The pioneering approach of Makela and Richardson (1977) and Smouse et al. (1990) exploited the Wahlund effect that a mixture of populations contains an excess of homozygotes and a deficiency of heterozygotes at any locus as compared with a single population in Hardy–Weinberg equilibrium. The information among multiple loci was modeled under the assumption of linkage equilibrium. The Hardy–Weinberg and linkage equilibrium (HWLE) conditions are quite plausible for large, panmictic populations that do not exchange immigrants; their genotype frequencies come into Hardy–Weinberg equilibrium in a single generation and approach linkage equilibrium at a geometric rate (e.g., Crow and Kimura 1970). A decade interlude in further recorded effort on methods for population mixture analysis with incomplete baselines attests to the level of the problem's challenge. The growth of Bayesian computational techniques, especially the Markov chain Monte Carlo (MCMC) method (Gilks et al. 1996), during the 1990s eventually encouraged reopening of the problem to improve on the solution offered by Smouse et al. (1990). In particular, the use of Gibbs sampling with the finite mixture model had been introduced to perform unsupervised cluster analysis of multivariate normal observations (Lavine and West 1992; Bensmail et al. 1997), and parallel applications for other probability distributions, including those for genotypes, were predictable. The term cluster is long-standing and is used interchangeably with the term subset hereafter, and cluster analysis will mean the statistical partitioning of a sample into disjoint and exhaustive subsets.

Pritchard et al. (2000) were first to extend the application of Gibbs sampling and the finite mixture model to include cluster analysis of multilocus genotype data. The cluster analysis could be performed in the complete absence of baseline samples, but partial baselines could also be included to increase precision and to provide a more informative analysis. Both source labels for mixture individuals as well as the genetic parameters of the populations present were estimated by a Bayesian treatment of the classification likelihood for the mixture genotypes. Although Pritchard et al. (2000) also considered possible hybrids in the mixture, our account is restricted to their treatment of mixture individuals from separately breeding populations. As had earlier authors, Pritchard et al. (2000) exploited the Wahlund effect in which Hardy–Weinberg and linkage disequilibrium among individuals of the mixture sample were interpreted as evidence for a mixture of populations. However, now the disequilibria were used to partition the mixture sample into subsets that met the HWLE conditions and were thereby indistinguishable from samples drawn from separate panmictic populations. The program STRUCTURE (http://pritch.bsd.uchicago.edu/; see Pritchard et al. (2000)) uses Gibbs sampling with Bayesian methods and the finite mixture model to search for these subsets. Except for neglecting to introduce parameters representing unequal mixture proportions from the possible sources, the algorithm of Pritchard et al. (2000) for genetic data paralleled that of Bensmail et al. (1997) for multivariate normal data. Both studies used Bayesian and MCMC methods with conjugate priors for unknowns. In STRUCTURE, a pair of steps is cycled to convergence. First, cluster (or source) labels are stochastically assigned to mixture individuals according to the posterior source probabilities of their genotypes. Ordinarily, the posterior source probabilities would be computed by Bayes' theorem, using the source proportions composing the mixture as the prior probabilities for the genotypes (e.g., Koljonen et al. 2005), but STRUCTURE computes restricted analogues as if the source populations all contributed equally to the mixture. Second, draws are made of unknown allele frequencies from their source distributions that have been updated by the assignments. In contrast with Pritchard et al. (2000), who only acknowledged the possibility, Bensmail et al. (1997) included a third step to sample the unknown source proportions of the mixture and used these values in computing the posterior source probabilities of their multivariate normal mixture observations. After convergence, the MCMC samples of the unknowns of both studies were considered drawn from their Bayesian posterior distribution.

Although Gibbs sampling has proven to be a powerful method to attack many challenging statistical problems (Gilks et al. 1996), its use for clustering may commonly fail to explore the full range of possible solutions (Celeux et al. 2000; Jain and Neal 2004). In theory, $\kappa!$ symmetric modes of the Bayes posterior distribution for source proportions and allele frequencies would occur if κ extra-baseline sources were specified and the Pritchard et al. (2000) Gibbs sampler performed correctly. However, their sampler does not mix well and tends to explore a single mode of the posterior distribution. Pritchard et al. (2000) view the poor mixing in a positive light because the label-switching problem of mixture posterior distributions (Diebolt and Robert 1994; Richardson and Green 1997; Stephens 2000) is averted. Label switching in the present context occurs when the labels for individuals of the extra-baseline populations in the mixture change during the MCMC sampling effectively without warning. No guarantee is made that label switching will not occur with the Gibbs sampler of Pritchard et al. (2000), but

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in practice its frequency is apparently low. The root cause for label switching is the invariance of the mixture genotype likelihood function for the extra-baseline source proportions and genotype frequencies under permutations of the source labels. Without prior information to distinguish among the extra-baseline populations, the corresponding prior distribution also will be the same for permutations of the labels, and the posterior distribution will be symmetric as well (Dawson and Belkhir 2001).

The failure of Gibbs sampling to explore the posterior distribution thoroughly may appear to avert the label-switching problem, but at the cost of reduced sensitivity for detecting populations in their mixtures. If the allele frequencies of two or more populations in the mixture are similar, the sampler may become trapped in a local mode for which too few populations are detected and the mixture individuals of some closely related populations are clustered together. Perhaps intended as a remedy, Falush et al. (2003) extended the modeling of Pritchard et al. (2000) by modifying the prior distribution for allele frequencies so that more-similar source populations were possible. However, the Gibbs sampler sorts the individuals stochastically one by one among clusters. In so doing, a composite cluster of individuals from similar populations is less likely to be separated into its components as rapidly as if all the individuals in the cluster were partitioned as a group into sweetened subsets, each of which is more consistent with HWLE conditions. Nonetheless, once most individuals of each population present have been correctly classified to separate, though possibly contaminated, clusters, the Gibbs sampler can be effective in refining them to purer source composition.

Dawson and Belkhir (2001) developed an MCMC sampler, implemented by their program PARTITION (http://www.univ-montp2.fr/~genetix/partition/partition.htm), that is based on the Metropolis–Hastings algorithm and is capable of group updates among clusters, including merging and splitting. However, when a cluster is split, the individuals are assigned at random to two non-empty subsets without regard to their genotypes. As noted by Jain and Neal (2004), although in a more general clustering context, the random split proposal is unlikely to be appropriate. An alternative recipe for clustering general data called the split–merge algorithm was developed by them which, like that of Dawson and Belkhir (2001), performs group updates among clusters, but uses the data for splitting. Later, our specialization of the split–merge algorithm to genetic data will also split clusters into subsets, but based on genotypes of the members so that the subsets are more likely to better satisfy the HWLE conditions.

The labeling problem must be dealt with when mixing is so improved that many, or even all, the modes of the posterior distribution are visited during sampling. The labels themselves become meaningless if more than a single extra-baseline population is allowed. If mixing were complete, the marginal posterior distributions of source proportions from the extra-baseline populations would be equal, as would those of their allele relative frequencies. Such identical distributions are useful only for inference about the combined extra-baseline population composition but are useless for any detail if several extra-baseline populations are present. Dawson and Belkhir (2001) proposed a practical solution after observing that the assignment of individuals to their source populations induces a partition of the mixture sample into disjoint, non-empty subsets and that the partition itself is the parameter of interest. The frequencies of random draws of particular partitions from their posterior distribution by a sampling algorithm could be used to quantify the evidence in favor of each. However, if the mixture sample is large and many individuals are difficult to assign, the number of plausible partitions will be so great that scrutinizing their evidence individually will be impractical. In this case, Dawson and Belkhir (2001) recommended additional processing of the partitions drawn by the sampler to identify clusters of mixture individuals whose joint assignments to subsets among the partitions are frequent. Co-assignment probabilities for all possible groups of a fixed number, say d, of mixture individuals were defined for use as similarity measures by which to perform the clustering. The co-assignment probability for any particular d group is the proportion of the partitions generated by the sampler for which all d members are included within single subsets of the partitions. Because the comprising subsets of the partitions are drawn to satisfy the HWLE conditions of separate populations, the co-assignment probability of a d group is viewed as the posterior probability that its members belong to the same population. Although the *size* of the d group is arbitrary, Dawson and Belkhir (2001) mainly used a pair of individuals ($d = 2$) for illustration and this choice is used hereafter. With the co-assignment probabilities determined for all possible pairs of mixture individuals, a hierarchical, agglomerative, model-free method called complete linkage was used by Dawson and Belkhir (2001) to group the mixture individuals into a binary tree of relatedness (e.g., see Fig. 1). Each internal node of the tree maps to a cluster of mixture individuals, any pair of which has co-assignment probability at least equal the node's ordinate. The ordinate is termed the minimum co-assignment probability for the associated cluster of mixture individuals, and when its value is high, a common source for the cluster members is indicated. Although the Dawson–Belkhir tree does not make complete use of the posterior distribution of mixture sample partitions, it provides a pragmatic compromise that solves the label-switching problem by referring the subsets of partitions back to the comprising mixture individuals. Furthermore, the tree is very helpful by providing an organizational chart of the mixture sample individuals separated into their comprising populations for every level of minimum co-assignment probability.

Despite noting that the problem of inferring the number of populations is difficult, Pritchard et al. (2000) make its estimation a central issue. To infer the number of HWLE subsets present, the authors derive an approximation of its Bayesian posterior distribution. However, the accuracy of the approximation is unknown, and the authors recommend the posterior distribution be used only as a rough guide to select the number of populations in the mixture. Although Pritchard et al. (2000) state that their posterior distribution for κ seems to give sensible answers in practice, Falush et al. (2003) are less sanguine, noting that determining κ is very difficult and that its estimates should be treated with caution because they may depend on the amount of variation expected among the populations a priori. In place of testing, the Dawson–Belkhir tree depicts for the decision maker the

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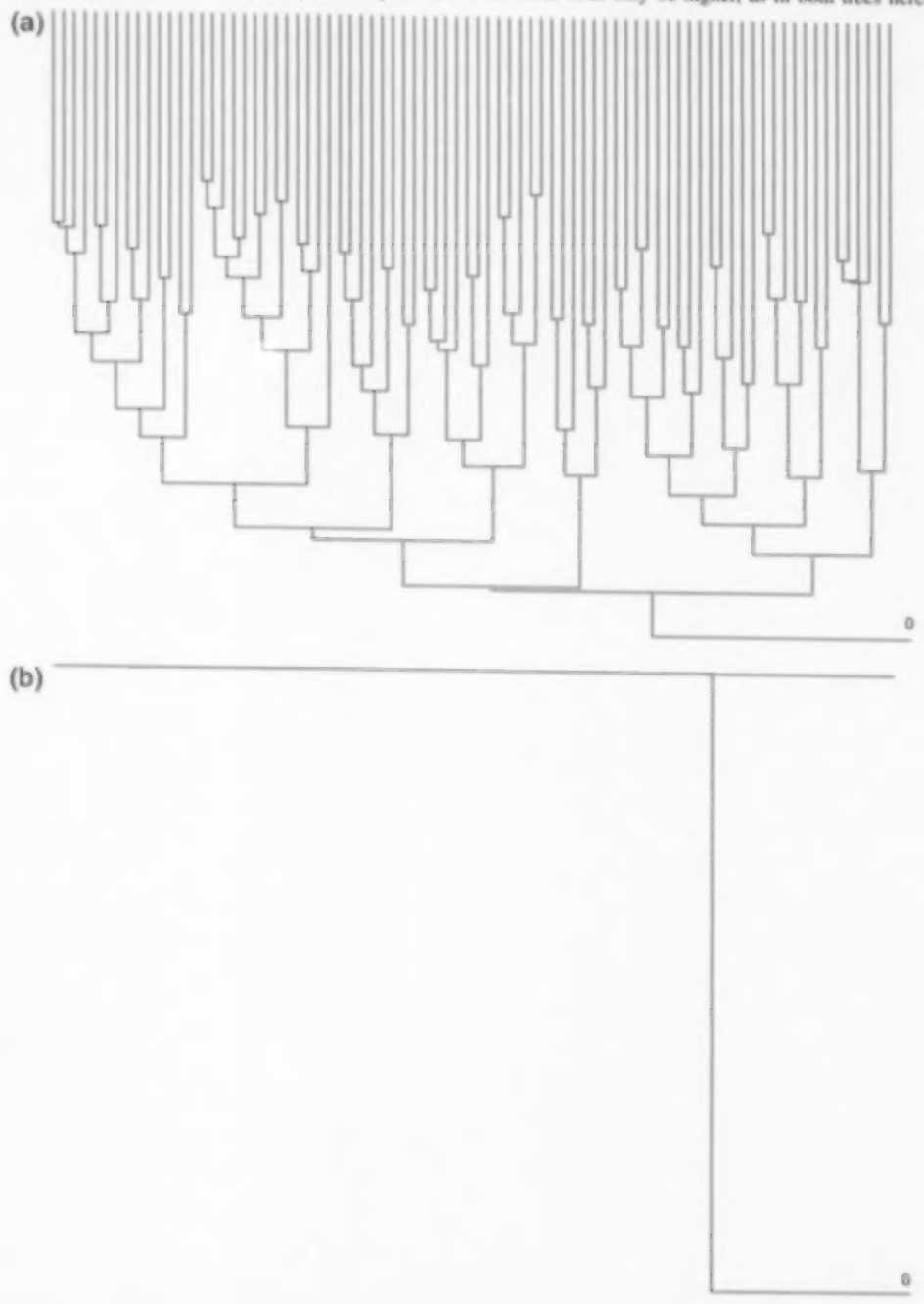
Fig. 1. Tree plots for artificial data set 5 (80 genotypes of individuals from a single source population) from (*a*) 10 000 PARTITION samples and (*b*) 10 080 HWLER samples. A tree is composed of M terminal nodes, which represent the M individuals of the mixture sample, and $M - 1$ internal nodes, each of which has two descendent nodes. A descendent node can be either a terminal or internal node. Every internal node corresponds to a cluster or subset of individuals that can be reached by the descendent nodes above it. Associated with an internal node is its height or probability level, which is the smallest co-assignment probability among any pair of individuals chosen from the cluster above it. Terminal nodes at the treetop have greatest height with unit probability level by definition. The tree is constructed sequentially by joining pairs of open nodes (i.e., nodes that are not yet descendents). At each step, a pair of open nodes is joined to form a new internal node, with the choice being the pair for which the new internal node has greatest height. The tree bottom has lowest height equal to zero probability level, and the final node may be higher, as in both trees here.



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plausible clusters with their associated, objectively determined, minimum co-assignment probabilities. Importantly, the sizes of these clusters are self-evident, which necessarily affects the consequence attached to the value of κ. Dawson and Belkhir (2001) generated the distribution of κ within their program PARTITION as the number of non-empty partition subsets. Despite its availability without approximation from the sample of partitions, the posterior distribution of κ was considered of passing interest in comparison with that of the mixture sample partition and the comprising members of its subsets. The reason that this posterior distribution was underplayed may have been its irregular performance among several applications that will be revisited later.

Next, we specialize the Gibbs and split–merge samplers of Jain and Neal (2004) to genetic data, including the improvement to splits suggested by Dahl (2003). In place of the finite mixture model, a nonparametric analogue called the Dirichlet process mixture model (Walker et al. 1999; Neal 2000; Müller and Quintana 2004) is the statistical foundation. A conjugate prior is used for the population allele frequencies, and as a result, only the partition of the mixture sample is drawn by the two samplers with the remaining unknowns integrated away. First, the mixture sample analysis without baseline samples of the separate source populations is described. Second, modifications of the algorithms to incorporate any baseline samples are detailed.

The Gibbs sampler for a genetic mixture without baseline samples

The mixture sample genotypes will be partitioned into HWLE subsets that are indistinguishable from several samples of separate source populations. The Bayes posterior distribution of partitions is key to evaluating the plausibility of the HWLE subsets. The list of genotypes for the M individuals of the mixture sample is denoted by $\boldsymbol{X} = (\boldsymbol{X}_1,\ldots,\boldsymbol{X}_M)$. The genotypes are determined from L independent loci with the hth locus having J_h different alleles among the source populations. The multilocus genotype of the mth individual is denoted by $\boldsymbol{X}_m = (\boldsymbol{X}_{m1},\ldots,\boldsymbol{X}_{mL})$, where $\boldsymbol{X}_{mh} = (x_{mh1},\ldots,x_{mhJ_h})$ is the vector of allele counts for individual m at the hth locus. In particular, the total count of alleles for the mth diploid individual at any locus h is $x_{mh+} = \sum_{j=1}^{J_h} x_{mhj} = 2$. Under HWLE conditions, the genotype $\boldsymbol{X}_m$ has the relative frequency in its source:

$$(1)\qquad F(\boldsymbol{X}_m|\boldsymbol{Q}_m) = \prod_{h=1}^{L}\left[2^{1-\delta_h(\boldsymbol{X}_m)}\prod_{j=1}^{J_h} q_{mhj}^{x_{mhj}}\right]$$

where q_{mhj} is the allele relative frequency in the source population from which the mth individual was obtained, and $\delta_h(\boldsymbol{X}_m)$ equals 1 if individual m is homozygous and equals 0 if it is heterozygous for locus h. The collection of allele relative frequencies at the L loci in the source from which the mth individual was obtained is denoted as $\boldsymbol{Q}_m$.

The sampling model assumed to underlie the HWLE subsets is a mixture of Dirichlet process (MDP). The MDP model replaces the finite mixture model and its problematic fixed number of source populations with a so-called countably infinite mixture model having an uncertain number of sources to be estimated from the mixture sample itself. In our specialization of the MDP model to genetic data, the collections of allele relative frequencies in the source populations from which the mixture individuals derive ($\boldsymbol{Q}_m$, $m = 1,\ldots,M$) are assumed to be independently drawn from a flexible, nonparametric distribution (G) that is centered on a parametric distribution (G_0). The so-called mixing distribution G is itself uncertain and is in turn assumed to be randomly drawn from a Dirichlet process prior (DP[$\alpha G_0(\boldsymbol{\beta})$]), which is a distribution over the space of distribution functions. The Dirichlet process prior distribution has two parameters. First, the total mass parameter α is a positive scalar that determines, among other things, the prior distribution for the number of source populations present in the mixture sample. Second, the base distribution $G_0(\boldsymbol{\beta})$ is a model of the variation in allele relative frequencies at loci among source populations and depends on an array of hyperparameters ($\boldsymbol{\beta}$).

The prior distribution for the number of source populations is analytically available from Ewens (1972), but it can also be generated by Monte Carlo from repeated sums of M independent Bernoulli random variables ($\xi_1,\ldots,\xi_M$), with probability of success for the mth variable of a sum being $\Pr(\xi_m) = \alpha/(\alpha + m - 1)$, $m = 1,\ldots,M$ (Tavaré and Ewens 1997). This prior distribution shifts toward more sources as α increases. At small values for α, say 0.001, the prior distribution obeys Ockham's razor and places a preponderance of probability (>0.99) on a single source for any sample size M in a range of interest (e.g., $10 \le M \le 1000$). At a larger α, say 10, nearly all prior probability (>0.97) occurs for numbers of sources exceeding 4 ($M = 10$), 10 ($M = 100$), or 23 ($M = 1000$). Intermediate values of α paired with M in the same range result in intervening prior distributions between those described. Arbitrarily large values for α are allowed. Therefore, good flexibility in the prior for number of sources in the mixture sample is available through specification of a value for α.

The total mass parameter α also determines how concentrated G is about the base distribution $G_0(\boldsymbol{\beta})$. As $\alpha \to +\infty$, $G \to G_0$, and the base distribution becomes the mixing distribution G for the $\boldsymbol{Q}_m$. Small values of α on the order of 1 allow G to deviate materially from G_0 and imply the base distribution does not represent the mixing distribution well.

The sampling plan for genotypes from a population mixture under the MDP model can be succinctly described by a Bayesian hierarchical model:

$$\boldsymbol{X}_m|\boldsymbol{Q}_m \sim F(\cdot|\boldsymbol{Q}_m),\quad m = 1,\ldots,M$$

$$(2)\qquad \boldsymbol{Q}_m|G \sim G,\quad m = 1,\ldots,M$$

$$G \sim \mathrm{DP}(\alpha G_0)$$

Further stages of hierarchy can be added to this model with priors for α and the hyperparameters $\boldsymbol{\beta}$ of G_0 if these variables are treated as unknowns. For example, given the evident importance of α to the analysis, specifying its value a priori may be troublesome if the number of source populations is highly uncertain. As is described later, Bayesian estimation using an uninformative prior for α can extract information in the mixture sample about its plausible values and so lessen, or even eliminate, the burden of its choice. As a signpost for the geneticist, locus components of the base

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distribution G_0 will be chosen shortly to be the familiar Rannala–Mountain equiprobable prior for allele relative frequencies with known hyperparameters $\boldsymbol{\beta}$ (see eq. 1 in Rannala and Mountain 1997).

The hierarchical model in eq. 2 can be viewed as a countably infinite mixture model, and when G is integrated over its DP(αG_0) prior distribution, the resulting distribution is a prior for the $\boldsymbol{Q}_m$ that is called a generalized Polya urn scheme (Blackwell and MacQueen 1973). In genetics, the same prior distribution results from the Ewens sampling formula that was independently discovered by Ewens (1972) for describing the probabilities of partitions of a sample of selectively neutral alleles by their various forms. Different parameterizations of this Polya urn scheme are described by Jain and Neal (2004) and Dahl (2003) for general data, and both are useful. We begin by specializing Jain and Neal's (2004) version to our genetic mixture problem to develop a prior distribution for the individuals' sources. If latent labels $\boldsymbol{c} = (c_1,\ldots,c_M)$ are defined that identify the (unknown) source populations of the mixture individuals, the Polya urn scheme for sampling the $\boldsymbol{Q}_m$ is equivalent to the following sequential prior for the source labels:

$$(3)\qquad P(c_m = c \mid c_1,\ldots,c_{m-1}) = \frac{n_{m,c}}{m-1+\alpha}, \quad \text{for } c \in \{c_j\}_{j<m}$$

$$P(c_m \neq c_j \text{ for all } j < m \mid c_1,\ldots,c_{m-1}) = \frac{\alpha}{m-1+\alpha}$$

where $n_{m,c}$ is the number of mixture individuals preceding the mth individual that have the same source population labeled c. The possibilities for the source label of the current, or mth, individual include labels previously seen, and these labels have probabilities proportional to their observed frequencies among the preceding individuals (upper equation). However, a new source is also possible with probability proportional to the total mass parameter α (lower equation). Because the M mixture individuals can be treated as exchangeable under Bayesian methods (i.e., an individual's index does not convey information about its genotype), any individual can be withheld, and the prior probabilities for its label at eq. 3 will depend on the labels of the remaining $M-1$ individuals. Jain and Neal (2004) exploit the exchangeability to derive a Gibbs sampling procedure on the labels. In the present genetic application, the Gibbs sampling procedure sequentially assigns the source labels to the individuals using the prior at eq. 3 together with the genotype distribution model at eq. 1 integrated over uncertainty in the allele relative frequencies for the possible sources. Later, the same Gibbs sampler is completed in the notation of Dahl (2003), which is introduced next, and then his improved version of the Jain and Neal (2004) split–merge sampler is provided.

Dahl expresses the generalized Polya urn model in terms of subsets of the mixture sample that correspond to the earlier source labels. The labels partition the indices of the mixture individuals, $\{1,2,\ldots,M\}$, by their κ-purported sources into exhaustive and mutually exclusive subsets, say $\boldsymbol{\eta} = \{S_1,\ldots,S_\kappa\}$, where $\cup_{j=1}^{\kappa} S_j = \{1,2,\ldots,M\}$, $S_i \cap S_j = \phi$ for all $i \neq j$, and $S_i \neq \phi$ for all i. Here, ϕ denotes the empty set. The individuals in any subset S_j are from the same source and their number is denoted by $|S_j|$. The corresponding parameterization for the collections of allele relative frequencies in the sources $\boldsymbol{Q}_m$, $m = 1,\ldots,M$, in terms of the partition, is $\boldsymbol{Q}_1,\ldots,\boldsymbol{Q}_\kappa$. First, Dahl's partition prior, which results from products of terms in eq. 3 with appropriate notation changes from labels to subsets, is

$$(4)\qquad P(\boldsymbol{\eta}) = \frac{\alpha^\kappa \cdot \prod_{j=1}^{\kappa} \Gamma(|S_j|)}{\prod_{i=1}^{M} (\alpha + i - 1)} \propto \alpha^\kappa \cdot \prod_{j=1}^{\kappa} \Gamma(|S_j|)$$

The gamma function $\Gamma(|S|)$ for integer argument $|S|$ equals $(|S|-1)!$. Second, the associated collection of allele relative frequencies $\boldsymbol{Q}_1,\ldots,\boldsymbol{Q}_\kappa$ are independently drawn from the base distribution G_0 under Dahl's parameterization. Dahl's hierarchical model corresponding to eq. 2 becomes

$$\boldsymbol{X} \mid \boldsymbol{\eta}, \boldsymbol{Q}_1,\ldots,\boldsymbol{Q}_\kappa \sim \prod_{i=1}^{M} F\left[\boldsymbol{X}_i \mid \sum_{j=1}^{\kappa} \boldsymbol{Q}_j \cdot I(i \in S_j)\right]$$

$$(5)\qquad \boldsymbol{Q}_1,\ldots,\boldsymbol{Q}_\kappa \mid \boldsymbol{\eta} \sim \prod_{j=1}^{\kappa} G_0$$

$$\boldsymbol{\eta} \sim P(\boldsymbol{\eta}) \text{ at eq. 4}$$

where $I(E)$ is the indicator for event E.

Dahl obtains the key partition posterior distribution $P(\boldsymbol{\eta}|\boldsymbol{X})$ using Bayes' rule as

$$(6)\qquad P(\boldsymbol{\eta}|\boldsymbol{X}) \propto P(\boldsymbol{\eta}) \cdot L(\boldsymbol{X}|\boldsymbol{\eta})$$

This distribution is needed later in computing the Metropolis–Hastings acceptance ratio in the split–merge sampler. The partition prior $P(\boldsymbol{\eta})$ is provided by eq. 4. The partition likelihood $L(\boldsymbol{X}|\boldsymbol{\eta})$ is the joint probability of the partition genotypes after uncertainty in allele relative frequencies is integrated away:

$$(7)\qquad L(\boldsymbol{X}|\boldsymbol{\eta}) = \prod_{j=1}^{\kappa} L(\boldsymbol{X}_{S_j})$$

where

$$(8)\qquad L(\boldsymbol{X}_S) = \prod_{m \in S} P_{<m,S}(\boldsymbol{X}_m) = \prod_{m \in S} \int F(\boldsymbol{X}_m|\boldsymbol{Q})\, dH_{<m,S}(\boldsymbol{Q})$$

Here $P_{<m,S}(\boldsymbol{X}_m)$ is a conditional, expected relative frequency of the genotype of the mth individual of the subset S in the common source shared with the other members, which is computed over uncertainty in the allele relative frequencies based on $m-1$ preceding individuals of the subset. The posterior distribution $H_{<m,S}(\boldsymbol{Q})$ for the allele relative frequencies of a subset is computed from the prior G_0 updated by the genotypes of the subset preceding that of the mth individual.

If the integration at eq. 8 can be done analytically, the partition posterior distribution at eq. 6 can be directly evaluated up to a normalizing constant. The Dirichlet distribution is conjugate to the multinomial distribution for allele counts in samples for any locus (e.g., see section 3.7 of Lange 1997), and a product of these distributions as a prior for $\boldsymbol{Q}$ makes this integration straightforward. The joint prior for $\boldsymbol{Q}$, or the density corresponding to G_0, will be the product of Dirichlet

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densities for the allele relative frequencies at each locus h, $h = 1,\ldots,L$, viz.

$$(9)\qquad dG_0(\boldsymbol{Q}) = \prod_{h=1}^{L} \text{Dirichlet}(\boldsymbol{q}_h; \beta_{h1},\ldots,\beta_{hJ_h}) = \prod_{h=1}^{L} \frac{\Gamma(\beta_{h1}+\cdots+\beta_{hJ_h})}{\Gamma(\beta_{h1})\cdots\Gamma(\beta_{hJ_h})} q_{h1}^{\beta_{h1}-1}\cdots q_{hJ_h}^{\beta_{hJ_h}-1}$$

The parameters of the prior $\boldsymbol{\beta}_0 = (\beta_{h1},\ldots,\beta_{hJ_h})$, $h = 1,\ldots,L$, are constants to be specified or else given a prior distribution at eq. 2 and eq. 5. In particular, the equiprobable distribution assumption (Rannala and Mountain 1997) that $\beta_{hj} = J_h^{-1}$, $j = 1,\ldots,J_h$, is used in later applications. This choice of the constants makes G_0 a low-information prior for the collections of allele relative frequencies of the partition subsets. The distribution $H_{<m,S>}(\boldsymbol{Q})$ for the allele relative frequencies of a subset in eq. 8 is computed from the base prior density $dG_0(\boldsymbol{Q})$ and the multinomial sample of allele counts among the individuals in the subset S preceding individual m. The result is

$$(10)\qquad dH_{<m,S>}(\boldsymbol{Q}) = \prod_{h=1}^{L} \text{Dirichlet}(\boldsymbol{q}_h; \beta_{h1} + d^{S}_{<m,h,1>},\ldots,\beta_{hJ_h} + d^{S}_{<m,h,J_h>})$$

where $d^{S}_{<m,h,j>}$ is the count of the jth allele at locus h among the individuals preceding the mth individual in the subset S. The integrals at eq. 8 can now be evaluated (see eq. 3.13 of Lange 1997) as

$$(11)\qquad \int F(\boldsymbol{X}_m|\boldsymbol{Q})\, dH_{<m,S>}(\boldsymbol{Q}) = \psi(\boldsymbol{X}_m, \boldsymbol{d}^{S}_{<m>}, \boldsymbol{\beta})$$

where $\boldsymbol{d}^{S}_{<m>} = (d^{S}_{<m,h,j>}, h = 1,\ldots,L; j = 1,\ldots,J_h)$, $\boldsymbol{\beta} = (\boldsymbol{\beta}_1,\ldots,\boldsymbol{\beta}_L)$, and the function ψ is defined for generic genotype $\boldsymbol{X}$, allele count array $\boldsymbol{d}$, and prior parameter array $\boldsymbol{\beta}$ as

$$(12)\qquad \psi(\boldsymbol{X},\boldsymbol{d},\boldsymbol{\beta}) = \prod_{h=1}^{L} 2^{1-\delta_h(\boldsymbol{X})} \times \frac{[\delta_h(\boldsymbol{X}) + \beta_{hj_1} + d_{hj_1}](\beta_{hj_2} + d_{hj_2})}{\left(1 + \sum_{j=1}^{J_h}\beta_{hj} + \sum_{j=1}^{J_h} d_{hj}\right)\left(\sum_{j=1}^{J_h}\beta_{hj} + \sum_{j=1}^{J_h} d_{hj}\right)}$$

In eq. 12, j_1 and j_2 are the indices of alleles present at locus h of $\boldsymbol{X}$. Equation 12 approximates usual formulas for estimating genotype relative frequencies under HWLE using allele counts if the prior parameters β_{hj} are negligible. The partition posterior distribution can now be evaluated from eq. 6 for use later in the split–merge sampler.

The Gibbs sampler of Dahl (2003) is detailed next in which the mixture individuals are serially and stochastically assigned to updated partitions of the mixture sample. Dahl defines $\boldsymbol{\eta}^{-m}$ to be the partition $\boldsymbol{\eta}$ of the mixture sample but with the mth individual removed. If the mth individual is a singleton in its partition subset, the corresponding empty subset is discarded. The computations can be started by arbitrarily partitioning the mixture sample. In later applications, the initial partition is a single subset composed of all the mixture individuals; that is $\kappa = 1$, $S_1 = \{1,2,\ldots,M\}$, and $\boldsymbol{\eta} = [S_1]$. (As an aside, the other extreme initial partition could as well have been chosen in which each individual composes a singleton subset, so that $\kappa = M$, $S_m = \{m\}$, $m = 1,\ldots,M$, and $\boldsymbol{\eta} = [S_1,\ldots,S_M]$.)

Then a Gibbs scan of the mixture sample comprises four steps for each individual $m = 1,\ldots,M$. First, remove the mth individual from the current partition $\boldsymbol{\eta}$ to obtain $\boldsymbol{\eta}^{-m}$. Second, for each $S \in \boldsymbol{\eta}^{-m}$, compute the full conditional probability for $m \in S$ by

$$\Pr(m \in S|\boldsymbol{\eta}^{-m}, \boldsymbol{X}) = b\cdot|S|\cdot\int F(\boldsymbol{X}_m|\boldsymbol{Q})\, dH_S(\boldsymbol{Q})$$

Third, compute the full conditional probability of a new singleton subset $\{m\}$ by

$$\Pr(m \in \{m\}|\boldsymbol{\eta}^{-m}, \boldsymbol{X}) = b\cdot\alpha\cdot\int F(\boldsymbol{X}_m|\boldsymbol{Q})\, dG_0(\boldsymbol{Q})$$

Fourth, assign the mth individual randomly with the probabilities at the second and third steps.

The probabilities at the second step are computed as though the mth individual was the last of each subset S because the individuals are considered to be exchangeable. Therefore, the posterior distribution $H_S(\boldsymbol{Q})$ is computed from G_0 and all the individuals of subset S, and its density is

$$dH_S(\boldsymbol{Q}) = \prod_{h=1}^{L} \text{Dirichlet}(\boldsymbol{q}_h; \beta_{h1} + d^{S}_{h,1},\ldots,\beta_{hJ_h} + d^{S}_{h,J_h})$$

where $d^{S}_{h,j}$ is the count of the jth allele of locus h among the individuals of subset $S \in \boldsymbol{\eta}^{-m}$. The integral at the second step is

$$\int F(\boldsymbol{X}_m|\boldsymbol{Q})\, dH_S(\boldsymbol{Q}) = \psi(\boldsymbol{X}_m, \boldsymbol{d}^{S}, \boldsymbol{\beta})$$

where the function ψ was defined at eq. 12, and $\boldsymbol{d}^{S} = (d^{S}_{h,j}, h = 1,\ldots,L; j = 1,\ldots,J_h)$. The integral at the third step is obtained from that at the second step by setting all the $d^{S}_{h,j} = 0$. The scalar b normalizes the values at the second and third steps so that the $(|\boldsymbol{\eta}^{-m}| + 1)$ full conditional probabilities sum to 1.

The sequentially allocated merge–split (SAMS) sampler for a genetic mixture without baseline samples

Jain and Neal (2004) introduced their split–merge sampler that uses the MCMC method with the Metropolis–Hastings algorithm to partition samples of general data. The Metropolis–Hastings acceptance probability is computed using eq. 6 and is chosen so that the chain of partitions from repeated random selection of subsets for splitting or merging converges to the partition posterior distribution $P(\boldsymbol{\eta}|\boldsymbol{X})$. The merge proposal is straightforward, with all individuals of a selected subset pair combined in a single subset. The split proposal is more complicated and is determined by a series of restricted Gibbs sampling scans to sweeten an initial random split of a selected subset. The split–merge algorithm is expected to rapidly separate heavily mixed subsets of individuals from several populations into purer components, but may be less efficient in sorting a few individuals among less contaminated subsets. To deal with fewer individuals, full Gibbs scans of the entire mixture sample are used alternately with the split–merge algorithm.

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Dahl (2003) suggested a promising improvement and simplification to the split–merge sampler of Jain and Neal. The repeated, restricted Gibbs sampling scans for the split proposal are replaced by a single, efficient split of the subset into two components by sequentially and stochastically allocating the individuals with probabilities updated from previous assignments of individuals of the subset. Dahl called this algorithm for general data the sequentially allocated merge–split (SAMS) sampler, and its steps in the genetic mixtures context follow. First, draw a pair of individuals, i and j, at random without replacement from $\{1,\ldots,M\}$. Second, if i and j both belong to one of the subsets, say S, of the partition $\boldsymbol{\eta}$, propose a split of S and corresponding new partition, $\boldsymbol{\eta}^{\text{split}}$ that has 1 more subset than $\boldsymbol{\eta}$. Otherwise, if i and j belong to different subsets of $\boldsymbol{\eta}$, go to the eighth step below. Third, begin the split by removing individuals i and j from S and form singleton sets $S_i = \{i\}$ and $S_j = \{j\}$. Fourth, randomly permute the list of the individuals remaining in S and let k index their order in the permuted list. Fifth, add the kth individual to S_i with probability

$$\Pr(k \in S_i \mid S_{i,<k}, S_{j,<k}, \boldsymbol{X}) = \frac{|S_{i,<k}| \cdot P(\boldsymbol{X}_k \mid S_{i,<k})}{|S_{i,<k}| \cdot P(\boldsymbol{X}_k \mid S_{i,<k}) + |S_{j,<k}| \cdot P(\boldsymbol{X}_k \mid S_{j,<k})} \tag{13}$$

where $P(\boldsymbol{X}_k \mid S_{i,<k}) = \psi(\boldsymbol{X}_k, \boldsymbol{d}^{S_{i,<k}}, \boldsymbol{\beta})$, $\boldsymbol{d}^{S_{i,<k}} = (d_{hj}^{S_{i,<k}},\ h = 1,\ldots,L;\ j = 1,\ldots,J_h)$, $d_{hj}^{S_{i,<k}}$ is the count of the jth allele at locus h among the preceding individuals of S_i, and $|S_{i,<k}|$ is the count of preceding individuals of S_i. Otherwise, add individual k to S_j. Sixth, set the variable z_k equal to i or j if the kth individual is assigned to set S_i or S_j, respectively. Seventh, after the assignments of individuals in S are complete, accept the split proposal $\boldsymbol{\eta}^{\text{split}}$ with probability equal to the Metropolis–Hastings ratio, and otherwise keep the partition $\boldsymbol{\eta}$ that preceded the split.

The Metropolis–Hastings ratio for the split equals (at most) 1 or the product of three individual ratios, viz.

$$\alpha(\boldsymbol{\eta}^{\text{split}} \mid \boldsymbol{\eta}) = \min\left[1, \frac{\rho(\boldsymbol{\eta} \mid \boldsymbol{\eta}^{\text{split}})}{\rho(\boldsymbol{\eta}^{\text{split}} \mid \boldsymbol{\eta})} \cdot \frac{P(\boldsymbol{\eta}^{\text{split}})}{P(\boldsymbol{\eta})} \cdot \frac{L(\boldsymbol{\eta}^{\text{split}} \mid \boldsymbol{X})}{L(\boldsymbol{\eta} \mid \boldsymbol{X})}\right] \tag{14}$$

where

$$\frac{\rho(\boldsymbol{\eta} \mid \boldsymbol{\eta}^{\text{split}})}{\rho(\boldsymbol{\eta}^{\text{split}} \mid \boldsymbol{\eta})} = \frac{1}{\prod_{k:z_k=i} \Pr(k \in S_i \mid S_{i,<k}, S_{j,<k}, \boldsymbol{X}) \cdot \prod_{k:z_k=j} \Pr(k \in S_j \mid S_{i,<k}, S_{j,<k}, \boldsymbol{X})}$$

with the denominator computed as the product of the sequence of assignment probabilities at eq. 13 for assignments actually chosen;

$$\frac{P(\boldsymbol{\eta}^{\text{split}})}{P(\boldsymbol{\eta})} = \alpha \cdot \frac{(|S_i|-1)!(|S_j|-1)!}{(|S|-1)!} \tag{15}$$

where α is the total mass parameter of the MDP model, and $|S_i|$ and $|S_j|$ are the final counts of individuals in the sets containing (and including) individuals i and j, respectively. Also, $|S| = |S_i| + |S_j|$ is the total number of these individuals and

$$\frac{L(\boldsymbol{\eta}^{\text{split}} \mid \boldsymbol{X})}{L(\boldsymbol{\eta} \mid \boldsymbol{X})} = \frac{\prod_{k \in S_i} P(\boldsymbol{X}_k \mid S_{i,<k}) \cdot \prod_{k \in S_j} P(\boldsymbol{X}_k \mid S_{j,<k})}{\prod_{k \in S} P(\boldsymbol{X}_k \mid S_{<k})}$$

with $P(\boldsymbol{X}_k \mid S_{i,<k})$ and $P(\boldsymbol{X}_k \mid S_{<k})$ as defined immediately below eq. 13. The order of individuals indexed by k in the denominator begins with i and j and is followed by the permuted order at the fourth step.

Eighth, if i and j belong to different subsets of $\boldsymbol{\eta}$, propose to merge the individuals in the same subsets as i and j (say S_i and S_j, respectively) to form the merged set $S = S_i \cup S_j$ of the partition $\boldsymbol{\eta}^{\text{merge}}$. Ninth, accept the merge proposal with probability given by the Metropolis–Hastings ratio and otherwise keep $\boldsymbol{\eta}$.

To compute the Metropolis–Hastings ratio for a merge, the device of an imaginary split from $\boldsymbol{\eta}^{\text{merge}}$ to $\boldsymbol{\eta}$ is used with the indices of the individuals randomly permuted before the split. The Metropolis–Hastings ratio equals (at most) 1 or the product of three individual ratios, viz.

$$\alpha(\boldsymbol{\eta}^{\text{merge}} \mid \boldsymbol{\eta}) = \min\left[1, \frac{\rho(\boldsymbol{\eta} \mid \boldsymbol{\eta}^{\text{merge}})}{\rho(\boldsymbol{\eta}^{\text{merge}} \mid \boldsymbol{\eta})} \cdot \frac{P(\boldsymbol{\eta}^{\text{merge}})}{P(\boldsymbol{\eta})} \cdot \frac{L(\boldsymbol{\eta}^{\text{merge}} \mid \boldsymbol{X})}{L(\boldsymbol{\eta} \mid \boldsymbol{X})}\right]$$

where

$$\frac{\rho(\boldsymbol{\eta} \mid \boldsymbol{\eta}^{\text{merge}})}{\rho(\boldsymbol{\eta}^{\text{merge}} \mid \boldsymbol{\eta})} = \prod_{k:z_k=i} \Pr(k \in S_i \mid S_{i,<k}, S_{j,<k}, \boldsymbol{X}) \cdot \prod_{k:z_k=j} \Pr(k \in S_j \mid S_{i,<k}, S_{j,<k}, \boldsymbol{X})$$

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which is the product of the sequence of assignment probabilities for hypothetical assignments that would be needed to obtain $\boldsymbol{\eta}$ when beginning from $\boldsymbol{\eta}^{\text{merge}}$:

$$(16)\quad \frac{P(\boldsymbol{\eta}^{\text{merge}})}{P(\boldsymbol{\eta})} = \frac{1}{\alpha}\cdot\frac{(|S|-1)!}{(|S_i|-1)!(|S_j|-1)!}$$

$|S_i|$ and $|S_j|$ are the beginning counts of individuals in the sets containing (and including) individuals i and j, respectively; and $|S| = |S_i| + |S_j|$; and

$$\frac{L(\boldsymbol{\eta}^{\text{merge}}|\boldsymbol{X})}{L(\boldsymbol{\eta}|\boldsymbol{X})} = \frac{\prod_{k\in S} P(\boldsymbol{X}_k|S_{<k})}{\prod_{k\in S_i} P(\boldsymbol{X}_k|S_{i,<k})\cdot\prod_{k\in S_j} P(\boldsymbol{X}_k|S_{j,<k})}$$

Hybrid Gibbs and SAMS algorithm

The Gibbs and SAMS samplers are used alternately to search for HWLE subsets among the mixture individuals. The program for this hybrid sampler will be called HWLER (ftp://ftp.afsc.noaa.gov/Sida/Mixture-analysis/HWLER/). The mass parameter α can be fixed throughout the search, or it can be estimated from the mixture sample. If actual knowledge or a preferred hypothesis concerning likely number of sources is available, choice of a corresponding fixed value for α can be aided by computing the prior distributions for the number of source populations over a range of α by analytical or Monte Carlo methods described earlier. Alternatively, the posterior distribution of α and the other unknowns can be generated during the MCMC sampling using an uninformative gamma prior for this parameter (MacEachern and Müller 1998). The SAMS sampler is run through n_s draws, and the Gibbs sampler is run through n_g scans of the mixture sample for each HWLER cycle. The notation HWLER (n_s,n_g) will be used to represent this choice for running the samplers. After the SAMS and Gibbs samplers have finished their draws and scans of a cycle, a draw of α, if appropriate, completes the cycle. A new cycle is begun using either the fixed value or the last draw for α. The SAMS sampler is applied to the most recent $\boldsymbol{\eta}$ from the Gibbs sampler, followed by the Gibbs sampler applied to the last $\boldsymbol{\eta}$ from the SAMS sampler.

Incorporating baseline samples

Baseline samples can be incorporated in the Gibbs and SAMS samplers. With baseline samples present, both samplers distinguish between partition subsets of the mixture sample that correspond to baseline versus extra-baseline populations. Also, both samplers act only to partition the mixture sample individuals to their separate sources and take the sources of the baseline individuals as known. The Gibbs sampler expands the single possibility for a new source of an individual when no baseline is available to include any of the baseline populations currently missing from the mixture partition as well as a new extra-baseline population. The prior probability for a new singleton subset when no baseline is available is evenly divided among the single extra-baseline and the several baseline possibilities when a baseline is available. The computations for the individual's genotype frequencies in its source possibilities include the samples of the baseline populations when applicable. The SAMS sampler merges and splits mixture partition subsets that coincidentally correspond to either baseline or extra-baseline populations. If a split of a mixture subset that corresponds to a baseline population is proposed by randomly drawing two of its members, then one of the individuals is randomly selected to remain associated with the baseline population while the other assumes a new extra-baseline source. On the other hand, a split proposed for an extra-baseline population proceeds as if no baseline samples were available. If a merge of two mixture partition subsets is proposed, none, one, or both subsets may be associated with baseline populations, and these three possibilities need to be dealt with if the merge is accepted. First, if neither subset is identified with a baseline population, the new merged subset is not identified with a baseline population. Second, if only one of the subsets is identified with a baseline population, then the merged subset is assigned to the same baseline population. Third and last, if both subsets are associated with baseline populations, then the merged subset is assigned to the baseline population corresponding to the larger subset. The detailed steps of the HWLER sampler with baselines are provided in Appendices A and B.

Applications: simulation samples, chickens, and Sashin Creek rainbow (*Oncorhynchus mykiss*) and steelhead (sea-run rainbow) trout

Three applications are presented below that compare the performance of HWLER to Pritchard et al.'s (2000) STRUCTURE or to Dawson and Belkhir's (2001) PARTITION and also illustrate some possible uses. The probabilistic detection of separate source populations and unaided identification of their members in the various mixture samples are of special interest. The posterior distribution for number of sources, κ, detected by a program is one basis for judging its performance. The nodes and associated clusters of its Dawson–Belkhir trees provide valuable detail. The program ANALYSE (http://www.univ-montp2.fr/~genetix/partition/partition.htm) from Dawson and Belkhir (2001) was used to compute co-assignment probabilities from HWLER's output. The program TreeView (http://taxonomy.zoology.gla.ac.uk/rod/treeview.html; Page 1996) was used to draw the binary trees. In all cases, an arbitrary choice of HWLER (2,5) was used, and no other values for numbers of SAMS draws and Gibbs scans per HWLER cycle were examined because partitioning of samples by HWLER was very computer-intensive and time-consuming.

In the first application, mixtures of unlabeled, artificial genotypes from one or two hypothetical populations that were generated by Dawson and Belkhir (2001) are revisited. Second, the microsatellite genotypes of individual chickens from 20 breeds (Rosenberg et al. 2001) are analyzed without their source labels as though the composite were a mixture sample. Both the hypothetical and chicken data sets are analyzed without baseline samples. Third and last, discovery of latent population structure and stock-mixture analyses with incomplete baselines are demonstrated for Sashin Creek rainbow and steelhead trout populations in Alaska (Thrower et al. 2004).

In each application, scans, splits, and merges by HWLER are repeated until convergence of the MCMC chain. Evi-

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dence for convergence includes stabilization of the distribution for the number of subsets κ over partitions in the chain and similarity of binary trees between early and late portions of the chain. If the chain is begun with a single partition subset as was done here, the magnitude of κ will initially increase as more HWLE subsets of individuals are discovered. Later in the chain, the growth of κ will reach an asymptote upon convergence about which it may vary thereafter. Retaining every *k*th sample and discarding the remainder thins the samples after the asymptote. The first and last halves of the thinned samples can be used to compute co-assignment probabilities for tree construction. Reasonable agreement of the trees will confirm that convergence occurred. Corresponding criteria for the analyses by PARTITION and STRUCTURE are available in the original references (Pritchard et al. 2000; Dawson and Belkhir 2001).

For completeness in description of the applications, the MDP mass parameter α is estimated by HWLER for each data set using an uninformative gamma prior with shape and scale parameters both set to 10^{-3}. The corresponding initial prior distributions for the numbers of partition subsets κ are generated by the method of composition: α is drawn from its gamma prior and source labels are drawn from the conditional Polya urn scheme given α. When repeated many times, the distribution of counts of distinct source labels provides the initial prior for κ with negligible Monte Carlo error. These initial prior distributions obey Ockham's razor and place a preponderance of probability on a single subset, but also allow positive probabilities for a wide range of κ. The posterior distributions of α that result are well behaved and are reflected in the posterior distributions for κ that are detailed below. Suffice to say here, larger posterior means for α of the data sets correspond to more sources. The extremes in posterior mean of α range from 0 for the single-source data sets of Dawson and Belkhir (2001) to 4.65 for the 20 chicken breeds of Rosenberg et al. (2001).

Example 1: artificial data sets from coalescent simulations (Dawson and Belkhir 2001)

The five artificial data sets were composed of 10-locus genotypes generated under either a single population model or else under a strong or weak divergence model for two source populations. Data set 1 was a composite sample of 200 genotypes from two populations under weak divergence with samples of 100 each. Data set 2 was a sample of 200 genotypes from a single population. Data set 3 was a composite sample of 80 genotypes from two populations under strong divergence with samples of 40 each. Data set 4 was a composite sample of 80 genotypes from two populations under weak divergence with samples of 40 each. Data set 5 was a sample of 80 genotypes from a single population. Data set 4 can be anticipated to be most challenging because of its combination of comparatively small sample size and weak divergence between two populations. In the analyses, HWLER drew a total of 100 800 partitions of each data set, and ANALYSE processed 10 080 of these partitions (second half of original draws after thinning by 5) to determine the posterior for κ and the binary trees.

Without exception, the numbers of sources present for the five data sets are better identified by HWLER than by PARTITION (Table 1). HWLER's posterior maxima coincide with the actual number of populations present, and in four of the five cases, these probabilities exceed 0.999. HWLER's posterior distribution for number of populations of the difficult data set 4 places greatest probability (probability = 0.767) on the actual value (2), but allows for one source more (probability = 0.233). However, HWLER's initial priors for the number of populations present in each data set place greatest probability (~0.99) on a single population (Table 1). Therefore, HWLER's posterior distributions for data sets 2 and 5 are simply confirming of the initial prior. Nonetheless, HWLER's posterior distributions for data sets 1, 3, and 4 contravene the initial prior. On the other hand, PARTITION's posterior maxima coincide with the actual number of populations only for data sets 1 and 2, whereas for data sets 3, 4, and 5, the maxima equal the upper bound of four sources specified for PARTITION by Dawson and Belkhir (2001). No bound on κ other than mixture sample size occurs in HWLER.

The binary trees from HWLER and PARTITION provide further detail in their performances, the interpretation of which will be easier after some preliminaries. A high ordinate at a node indicates the associated individuals are from a single population. A low ordinate at a node indicates that not all associated individuals are from the same population. Because either one or two populations were present in the samples for data sets 1 through 5, two kinds of trees are expected. If a single population occurs, the tree should be high-crowned, remaining simple and unbranched below its bottom node that has a high ordinate. If two populations occur, the tree should bifurcate at the bottom node that has a low ordinate, and the two branches should each be composed exclusively of individuals from the separate sources. Each of the two branches should remain simple and unbranched below their bottom node that has a high ordinate.

Relying more on the trees for determining the numbers of sources present than on the posterior distribution for κ, Dawson and Belkhir (2001) judged that PARTITION's trees for data sets 1 and 2 (neither shown) and 5 (Fig. 1*a*) were consistent with the sources present, the tree for data set 3 (Fig. 2*a*) indicated possibly one more source than the two present, but the tree for data set 4 did not support a bipartition expected (Fig. 3*a*). Corresponding HWLER trees for all data sets were at least as evocative of the number of populations present and in some cases more so. HWLER trees for single-source data sets 2 (not shown) and 5 (Fig. 1*b*) were simple and high-crowned and both with lowest node ordinates equal to 1. HWLER trees for two-source data sets 1 (not shown), 3 (Fig. 2*b*), and 4 (Fig. 3*b*) bifurcated at the bottom node with ordinate zero, and the two branches had bottom nodes with ordinates of 0.56 and 0.55 for data set 1, 1 and 1 for data set 3, and 0.53 and 0.48 for data set 4. Data set 4 seemed to include an artifactual mixed-source cluster of two individuals. Regardless of other effects, the two main branches of both programs' trees for data sets 1, 3, and 4 separated the individuals to the two populations quite accurately. The programs correctly partitioned either 194 or 195 of the 200 individuals of data set 1; that is, only six of the 200 individuals were reassigned by HWLER's tree to membership in the alternative cluster to that of their population, as compared with five individuals for PARTITION. The bipartitions of both programs correctly partitioned 80 of

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Table 1. The prior and posterior distributions of the number of source populations (κ) for Dawson and Belkhir's (2001) artificial data sets 1 through 5 from programs PARTITION (P) and HWLER (H).

Data set (actual κ)	Program	Distribution	κ				
			1	2	3	4	>4
1 (2)	P	Prior	0.250	0.250	0.250	0.250	0.000
		Posterior	0.349	0.604	0.043	0.004	0.000
	H	Prior	0.991	0.002	<0.001	<0.001	0.006
		Posterior	0.000	>0.999	<0.001	0.000	0.000
2 (1)	P	Prior	0.250	0.250	0.250	0.250	0.000
		Posterior	0.976	0.018	0.006	0.000	0.000
	H	Prior	0.991	<0.001	<0.001	<0.001	0.007
		Posterior	1.000	0.000	0.000	0.000	0.000
3 (2)	P	Prior	0.250	0.250	0.250	0.250	0.000
		Posterior	0.000	0.004	0.054	0.942	0.000
	H	Prior	0.990	0.002	0.001	<0.001	0.007
		Posterior	0.000	>0.999	<0.001	0.000	0.000
4 (2)	P	Prior	0.250	0.250	0.250	0.250	0.000
		Posterior	0.002	0.004	0.030	0.964	0.000
	H	Prior	0.992	0.001	<0.001	<0.001	0.006
		Posterior	0.000	0.767	0.233	0.000	0.000
5 (1)	P	Prior	0.250	0.250	0.250	0.250	0.000
		Posterior	0.006	0.004	0.030	0.960	0.000
	H	Prior	0.990	<0.001	<0.001	<0.001	0.008
		Posterior	1.000	0.000	0.000	0.000	0.000

Note: Values for PARTITION were reported by Dawson and Belkhir (2001) when using their parameters $r = 4$, $u = 1$, and $\theta = 1$.

80 individuals for data set 3, while PARTITION had 78 of 80 and HWLER had 79 of 80 individuals correctly partitioned for data set 4.

Example 2: 20 European chicken breeds (Rosenberg et al. 2001)

Rosenberg et al. (2001) genotyped 600 chickens (http://rosenberglab.bioinformatics.med.umich.edu/poultry.html) for 27 microsatellite loci (2–41 alleles per locus). The chickens were chosen from 20 European breeds (identified below by the original numeric codes assigned to them by the authors) known to be genetically isolated from each other for at least 20–50 generations. The authors applied the program STRUCTURE to the unlabeled individuals to demonstrate the capacity of genetic cluster analysis to discover the breeds unaided by any baseline information. Here HWLER is applied to the same data set for comparison. Using STRUCTURE, Rosenberg et al. (2001) concluded that at most 19 breeds could be usefully detected among the 20 breeds present. In reaching this decision, the authors repeatedly partitioned the unlabeled chickens with STRUCTURE using different proposals for the maximum number of sources ranging from 1 to 23. Having chosen the maximum number of sources, 100 runs of STRUCTURE were applied to the 600 unlabeled chickens, each run identifying a potentially different partition of individuals. At any run, each chicken was assigned to a single breed using a multistep algorithm to deal with hybrids and mixed-breed subsets. (Notice that the application of STRUCTURE permitted hybrids, which are implicitly assumed absent with HWLER, and that assumption, if valid, could favor performance by HWLER.) According to the algorithm, if a subset identified by STRUCTURE contained multiple breeds, then the subset was further partitioned with STRUCTURE. In practice, of course, this information required by the algorithm about the breed composition of clusters is unavailable. As a consequence of specifying only 19 possible partition subsets for the 20 breeds, every partition included at least one mixed-breed subset. Rosenberg et al. (2001) found that across all 100 runs of STRUCTURE, a total of five breeds (4, 19, 27, 32, and 102) always fell into their own subsets and 11 more breeds (5, 13, 16, 21, 26, 28, 33, 42, 50, 51, and 3402) often (67%–99% of the time) did so as well. However, breeds 44 and 45 always shared the same subset, and breeds 18 and 37 were often (53% of time) together in a single subset.

HWLER was run for a total of 24 500 draws on the chicken data, each draw representing a potentially different partition. The degenerate posterior distribution for number of HWLE subsets had all mass concentrated at 23, thereby contravening the initial prior distribution that placed probability of ~0.99 on a single breed. The software ANALYSE processed 1225 of these partitions (second half of 24 500 samples thinned by 10) and clustered the individuals into a binary tree. The tree, displayed with the software TreeView (Page 1996), partitioned the chickens into 23 clusters at ordinate, or minimum co-assignment probability, of 0.651. The

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Fig. 2. Tree plots for artificial data set 3 (80 genotypes of individuals, 40 from each of two populations, generated under strong divergence) from (*a*) 10 000 PARTITION samples and (*b*) 10 080 HWLER samples. See Fig. 1 for explanation of a tree plot.

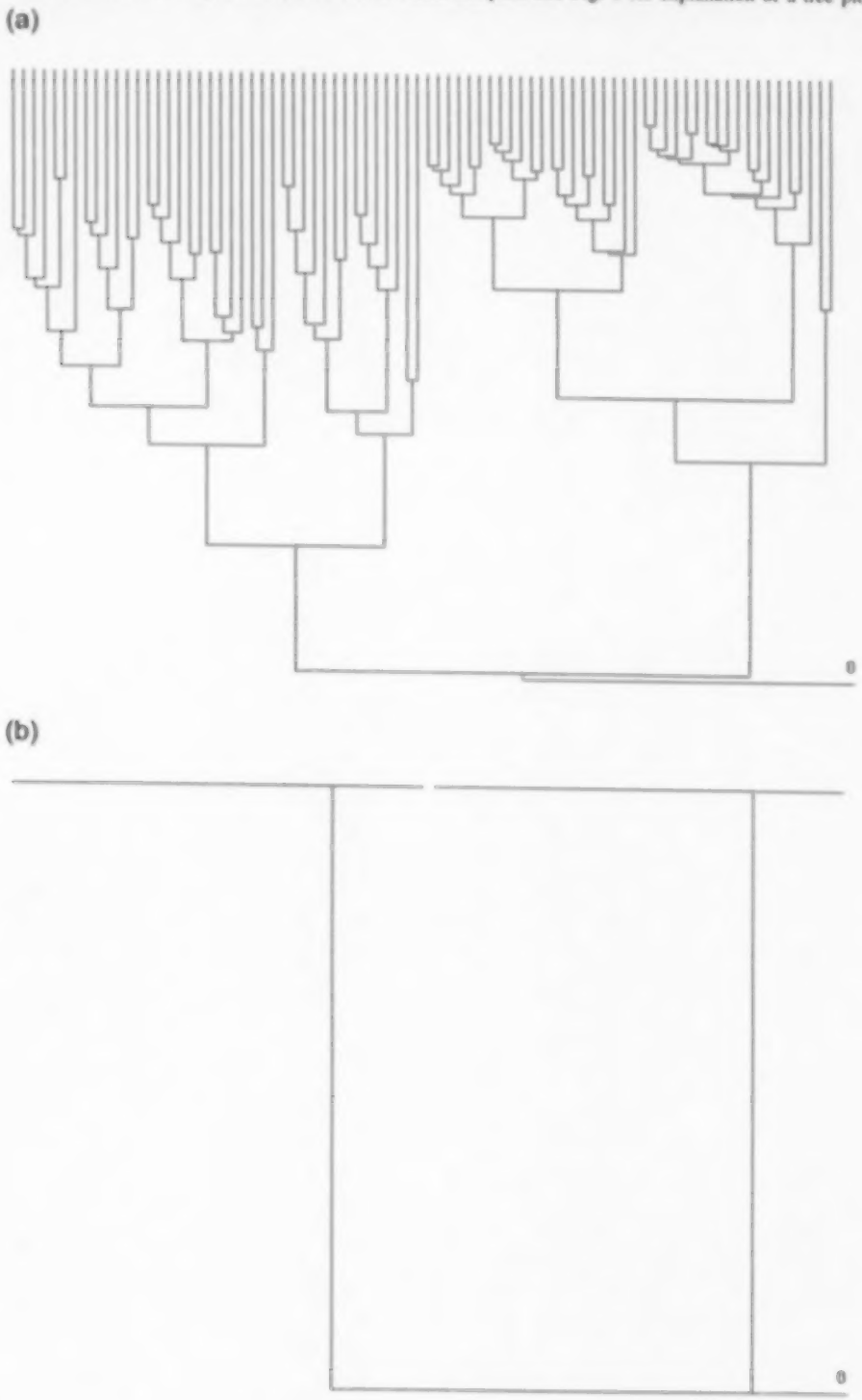

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Fig. 3. Tree plots for artificial data set 4 (80 genotypes of individuals, 40 from each of two populations, generated under weak divergence) from (*a*) 10 000 PARTITION samples and (*b*) 10 080 HWLER samples. The bipartition identified in both trees missorted individual 23 with population 2. In addition, the bipartition identified in PARTITION's tree missorted individual 73 with population 1. See Fig. 1 for explanation of a tree plot.

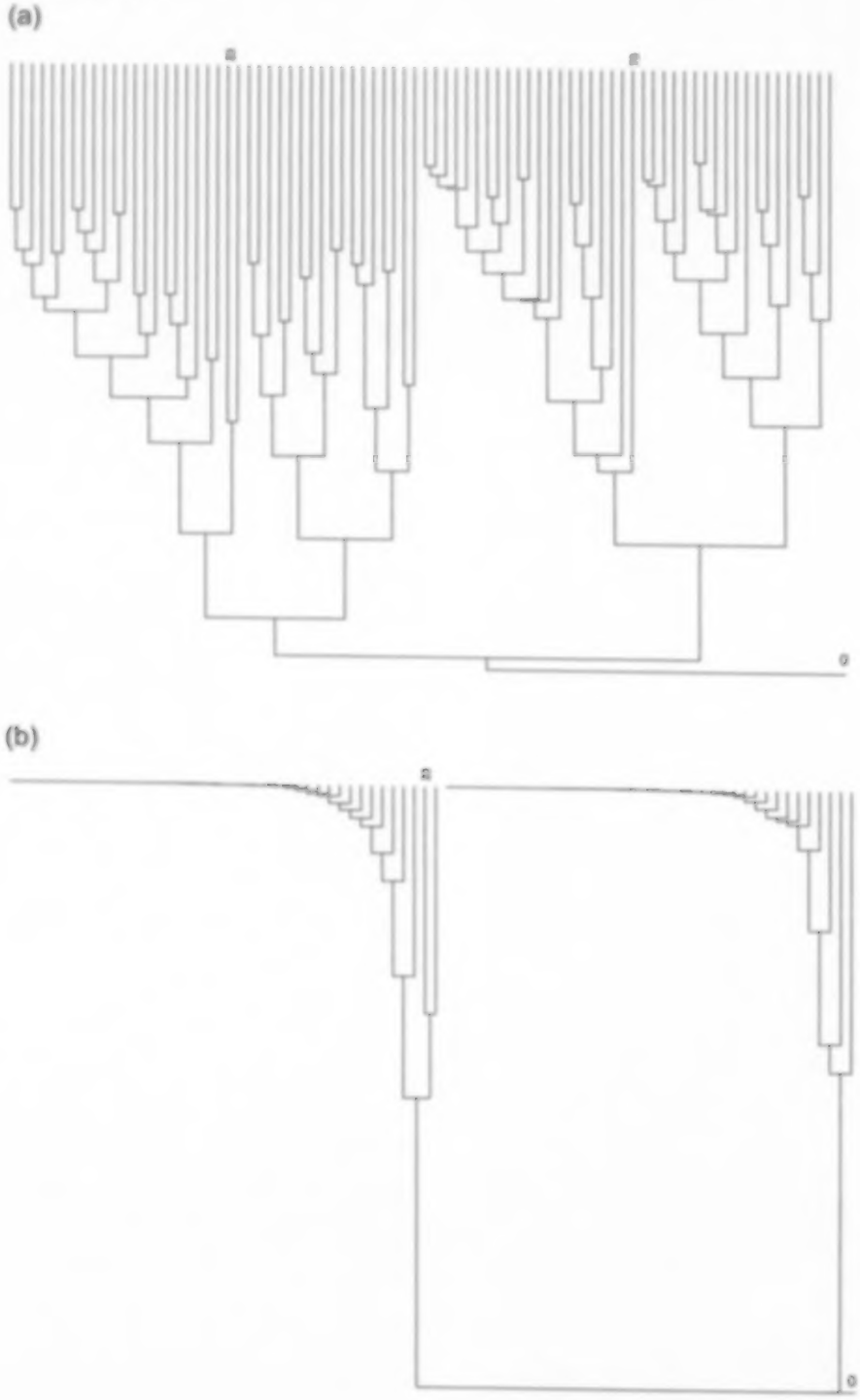

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Table 2. The posterior distributions of the number of extra-baseline populations (κ) for Sashin Creek watershed sampling locations.

		κ					
Sampling location	Sample size	0	1	2	3	4	≥5
Sashin Lake	60	—	0.999	<0.001	<0.001	<0.001	<0.001
Round Lake	60	—	0.000	<0.001	0.771	0.199	<0.030
Middle Sashin Creek	76	0.435	0.260	0.212	0.083	0.009	<0.001
Lower Sashin Creek	59	<0.001	0.003	0.051	0.264	0.503	>0.175

Note: Sashin Lake and Round Lake samples were analyzed without baseline samples, whereas middle and lower Sashin Creek samples were analyzed with four baseline samples, namely Sashin Lake and Round Lake A, B, and C.

results described next pertain to these 23 clusters. Sixteen breeds (4, 5, 13, 16, 18, 19, 26, 27, 28, 32, 33, 37,42, 50, 51, and 3402) of 30 chickens each were correctly partitioned into their exclusive clusters at high minimum co-assignment probabilities that averaged 0.973 per breed (range: 0.651–0.999). Only 1 of these 16 breeds had minimum co-assignment probabilities less than 0.940, and that breed included a single individual responsible; the remaining 29 individuals had minimum co-assignment probability greater than 0.972. Individuals of breeds 44 and 45 shared the same cluster at high minimum co-assignment probability of 0.999. The extra clusters that are inferred from HWLER's posterior distribution for number of subsets can be attributed to partitioning two breeds (21 and 102) into multiple clusters, each composed of a single breed. In particular, HWLER partitioned Mediterranean breed 21 into two clusters (14 and 16 chickens) and feral breed 102 into four clusters (1, 1, 3, and 25 chickens). The fidelity of the individual assignments to these additional clusters was high, with the average minimum co-assignment probabilities for the clusters in breeds 21 and 102 equaling 0.998 and >0.999, respectively. HWLER's partitioning of these single breeds into multiple clusters may be evidence of further genetic isolation among individuals within breeds. For example, three individuals of breed 102 identified by HWLER as a single cluster were sampled from a zoo flock that was speculated by Rosenberg et al. (2001) to have undergone genetic drift. The fact that STRUCTURE did not further subdivide these same two breeds may not contradict HWLER's results because the algorithm (Rosenberg et al. 2001) discontinued additional partitioning of any clusters closely associated with a single breed.

Because breeds 44 and 45 were combined by HWLER when all 600 chickens of 20 breeds were present in the composite sample, their analysis was repeated. First, the composite was limited to the 60 chickens of the pair. Although the initial prior again placed most probability on a single breed, the posterior distribution for number of subsets was concentrated at 2 (probability = 0.988) with a maximum of 3. HWLER correctly partitioned individuals of the two breeds except for one individual of breed 45 that was included with breed 44. Except for that individual, individuals of breeds 44 and 45 had minimum co-assignment probabilities of 0.856 and 0.994, respectively. Interestingly, the misassigned chicken was also incorrectly placed by STRUCTURE in the same pair-wise analysis (Rosenberg et al. 2001). Second, the other extreme initial partition was used to begin HWLER's sampling of partitions for the 600 chickens (*i.e.*, $\kappa = 600$, $S_m = \{m\}$, $m = 1,\ldots,600$, and $\eta = \{S_1,\ldots,S_{600}\}$. The partition distribution was virtually the same, including complete confounding of breeds 44 and 45 into a single cluster.

Example 3: Sashin Creek steelhead stock mixture (Thrower et al. 2004)

Sashin Creek on Baranof Island in Southeast Alaska supports an anadromous, wild steelhead population in its lower portion. Sashin Creek drains Sashin Lake to the estuary and has a middle section separated above and below by barrier falls. Round Lake has an outlet stream to the middle section of Sashin Creek with another, higher, barrier falls. The rainbow trout population in Round Lake was established in 1938 with transplants from the Sashin Lake population, which itself originated as a single transplantation from the anadromous portion of Sashin Creek in 1926 (Thrower et al. 2004). Although all the falls prevent upstream migration of adults, at least some juvenile downstream migrants from the upper watershed apparently survive to enter the estuary and mature in the ocean. Therefore, mature anadromous steelhead in lower Sashin Creek are thought to be composed of a mixture of individuals from the upper watershed and the lower anadromous population. Thrower et al. (2004) found variation in 10 microsatellite loci (3–24 alleles per locus) among steelhead and rainbow trout. The authors genotyped 59 mature adults that returned to lower Sashin Creek in 1996, 76 juveniles from the middle section of Sashin Creek, and 60 juveniles from each of Sashin Lake and Round Lake. Part of these data previously illustrated a simplified, incomplete baseline, mixed-stock analysis of the lower Sashin Creek adults (Pella and Masuda 2001). To simplify, the adults were assumed to be a mixture from two populations: an upper watershed population represented by a pooled sample of the Sashin Lake and middle Sashin Creek juveniles and the extra-baseline, lower, anadromous population. Here we revisit the same data with HWLER, but now including the Round Lake samples that were previously unavailable.

First, HWLER was run for 420 000 partitions (210 000 for burn-in, last 210 000 for posterior distribution) of each of the Sashin Lake and Round Lake samples. The posterior distribution for κ in Sashin Lake was concentrated at one population with maximum probability = 0.999, but for Round Lake the distribution peaked at three populations with probability = 0.771, and nearly all the mass occurred between three and five populations (Table 2). The Sashin Lake tree was simple and high crowned, with lowest ordinate nearly equal to 1.0 (Fig. 4*a*). On the other hand, the Round Lake tree trifurcates at lowest ordinates of about zero, and the

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Fig. 4. Tree plots from 26 250 HWLER partitions (a longer burn-in was used for tree plotting so as not to exceed memory limits of ANALYSE) of the samples of size 60 from each of (*a*) Sashin Lake and (*b*) Round Lake. See Fig. 1 for explanation of a tree plot.

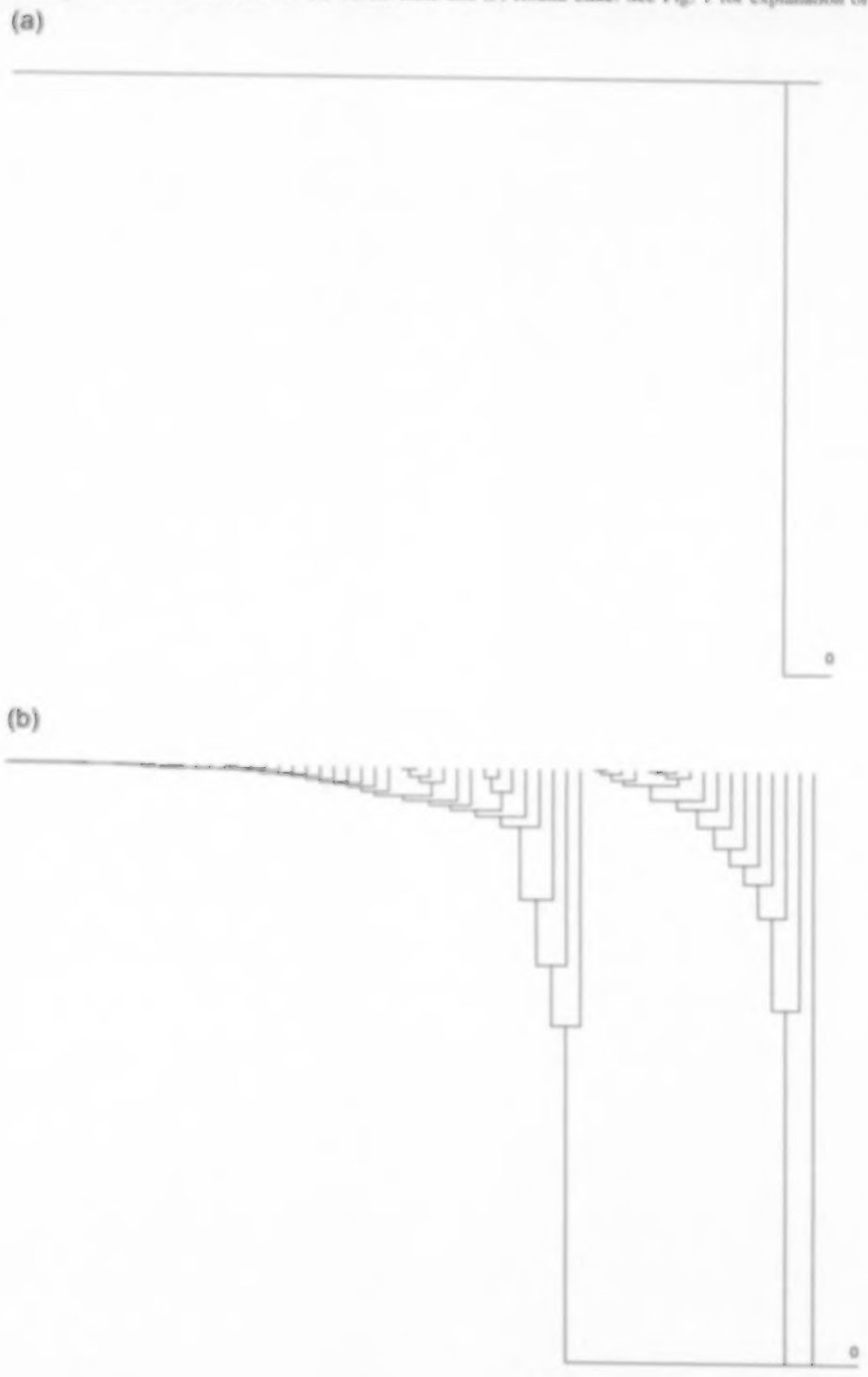

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Table 3. Parameters of the posterior density for population proportions of middle Sashin Creek juveniles (n = 76).

			Posterior quantiles*		
Population	Mean	SD*	2.5%	Median	97.5%
Round Lake A (n = 43)	<0.01	<0.01	0.00	0.00	0.01
Round Lake B (n = 16)	<0.01	<0.01	0.00	0.00	0.00
Round Lake C (n = 1)	0.00	<0.01	0.00	0.00	0.00
Sashin Lake (n = 60)	0.88	0.11	0.64	0.84	1.00
Extra-baseline clusters	0.12	0.11	0.00	0.14	0.34

Note: Parameters were calculated from 105 000 (840 000 thinned by 4 and 105 000 for burn-in) HWLER samples. SD, standard deviation.
*Uncertainty in the source composition of the Round Lake sample is not included.

Table 4. Parameters of the posterior density for population proportions of lower Sashin Creek anadromous adults (n = 59).

			Posterior quantiles*		
Population	Mean	SD*	2.5%	Median	97.5%
Round Lake A (n = 43)	<0.01	0.01	0.00	0.00	0.03
Round Lake B (n = 16)	<0.01	<0.01	0.00	0.00	0.02
Round Lake C (n = 1)	0.01	0.07	0.00	0.00	0.05
Sashin Lake (n = 60)	0.17	0.03	0.12	0.17	0.24
Extra-baseline clusters	0.81	0.08	0.73	0.83	0.86

Note: Parameters were calculated from 105 000 (840 000 thinned by 4 and 105 000 for burn-in) HWLER samples. SD, standard deviation.
*Uncertainty in the source composition of the Round Lake sample is not included.

three branches A (n = 43), B (n = 16), and C (n = 1) remain simple and unbranched until their lowest nodes that have ordinates of 0.57, 0.60, and 1.0, respectively (Fig. 4*b*). The more complex population structure of rainbow trout in Round Lake as compared with Sashin Lake was completely unexpected given that Round Lake is much smaller and was transplanted from Sashin Lake. Inlet and outlet streams of Round Lake are now suspected of providing sufficiently distinct spawning habitat for the transplant to fragment into separate populations.

Second, HWLER was run for 840 000 (thinned by 4 and 105 000 for burn-in) partitions of each of two samples — unlabeled middle Sashin Creek juveniles (n = 76) and unlabeled lower Sashin Creek adults (n = 59) — with baseline samples for Sashin Lake and the three branches for Round Lake. The posterior distribution for number of extra-baseline populations of the juveniles ranged from 0 to 4, with a maximum at 0 equal to 0.44 (Table 2) (i.e., the probability is 0.56 of one or more extra-baseline populations). Sashin Lake was the source for most (posterior average proportion of 0.88) of Sashin Creek juveniles; Round Lake juveniles were absent or in very low abundance (<0.01); and an unexpected extra-baseline contribution (0.12) may also have been present (Table 3). The posterior distribution of number of extra-baseline populations of the adults (Table 2) ranged from 2 to 5 or more, with a maximum at 4 equal to 0.50. In comparison with the juveniles, the adults were composed less of the Sashin Lake source (posterior average proportion of 0.17), about the same of the minor Round Lake component (<0.01), but more of extra-baseline populations (posterior average pooled proportion of 0.81) (Table 4). Based also on the microsatellite data, and reasonably consistent with these results, Pella and Masuda (2001) had found the upper watershed to contribute only 0.24 (95% posterior bounds of 0.13 and 0.37) of the lower Sashin Creek adults with the remainder from the anadromous population. The posterior distribution for number of extra-baseline populations of adults was unanticipated for the large number apparently present; biologists expected a single extra source rather than four, as suggested by the maximum. The estuary may be a mixing area of populations outside Sashin Creek, but adding baseline samples for populations of nearby watersheds did not point to their presence. The small contributions from Round Lake of juveniles of middle Sashin Creek and of adults in the estuary provide no evidence that the Round Lake fish survive the high falls to Sashin Creek.

Discussion

The compositions of population mixtures and source identification of individuals are commonly estimated from genetic data. Standard likelihood and Bayesian methods of estimation require baseline samples taken from every population present. If extra-baseline sources occur, such composition estimation may well be biased. To detect and estimate contributions from additional sources, several algorithms are described that all exploit HWLE conditions as expected for large, panmictic populations. First, Smouse et al. (1990) proposed sequential hypothesis testing for extra-baseline sources and likelihood estimation when detected. This approach requires several, possibly onerous, decisions of the analyst, including the particular order of tests for presence of the possible subsets of baseline and extra-baseline populations, choice of size of test and associated critical values for rejection of hypotheses, and what to do about probable bias in composition estimation related to size and power of tests.

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The recipe has not been applied widely, but has motivated later methods by revealing the power of the HWLE conditions for detecting extra-baseline sources.

Second, Pritchard et al. (2000) devised a Gibbs sampler to explicitly partition the mixture sample into HWLE subsets from a specified fixed number of separate sources. Only mixtures of purebreds are considered here, although the modeling of Pritchard et al. (2000) included hybrids. Partial or even completely missing baselines were allowed. However, this Gibbs sampler, which is implemented by their program STRUCTURE, requires repeated application of the program to a mixture sample by specifying different values for the unknown number of sources present to approximate its posterior distribution. Even then, accuracy of the posterior approximation for the number of sources is unknown. Furthermore, Gibbs sampling does not thoroughly explore the posterior distribution of the possible partitions of the mixture sample. Poor exploration results from the sequential assignment of individuals to subsets one at a time.

Third, Dawson and Belkhir (2001) developed an MCMC sampler that included set or group operations of splitting and merging. Group operations can be expected to result in better exploration of the posterior partition distribution. The sampler, implemented in their program PARTITION, generates the posterior distribution for the number of sources at a single application to the mixture sample. The improved exploration comes at the cost of label switching, in which the identities of extra-baseline subsets cannot be tracked. To remedy label switching, Dawson and Belkhir (2001) constructed a binary tree of the mixture individuals from their co-assignment probabilities by which to identify subsets from separate populations. However, Dawson and Belkhir's (2001) splitting proposal is completely random, which is unlikely to lead to improved splits of separate sources in subsets.

Fourth, the split–merge algorithm of Jain and Neal (2004) can be used with its sweetened splitting proposal that more likely partitions heavily mixed subsets into separate sources. On the other hand, the sequential assignments of single individuals to subsets by a Gibbs sampler should be more efficient than group assignments in refining subsets that contain only few individuals of mixed sources. Jain and Neal (2004) recommend alternating their split–merge sampler with a Gibbs sampler to most effectively separate observations of different sources for general data. Dahl (2003) simplified and improved upon the split–merge sampler with his SAMS sampler. In place of Jain and Neal's (2004) sweetening by repeated splits of a selected subset, Dahl (2003) more efficiently sweetens at a single pass. Here we specialize the Gibbs and SAMS samplers for application to genetic data and alternate them during sampling cycles. The program HWLER cycles the two samplers to discover HWLE subsets in the genetic mixture sample. Only source labels are drawn, and uncertainty in the genotype distributions among sources is integrated away. The posterior distribution for number of sources is generated at a single application to the mixture sample. Dawson–Belkhir binary trees are used to remedy label switching using co-assignments for all possible pairs of mixture individuals.

The program HWLER was applied to simulated and real genetic data sets to illustrate its use and describe their population structures for comparison with the programs PARTITION and STRUCTURE. The five simulated data sets allowed comparison of HWLER with PARTITION. Two simulated data sets had genotypes from a single hypothetical source, and three data sets had genotypes from two hypothetical sources. The maxima of the posterior probability distributions for the number of sources produced by HWLER consistently reflected the actual numbers present, whereas the maxima from PARTITION were less reliable. Nonetheless, the binary trees from both programs generally identified the individuals' sources with high accuracy even if some trees from PARTITION were less evocative of the sources present than those from HWLER. Likely PARTITION had not been run to convergence, as was also the case for HWLER when initially applied to the chicken data.

For the chicken data, HWLER's posterior distribution for number of sources placed all mass on 23 populations despite the purported presence of only 20 chicken breeds; additional population structure may have developed if reproductive mixing of any breed was poor. The corresponding tree correctly partitioned the 30 chickens of each of 16 breeds into exclusive clusters, further partitioned two of the breeds into multiple (two and four) clusters, and left 60 chickens of two breeds as a single, unresolved cluster. When the unresolved cluster was analyzed separately, the presence of two breeds was detected, and 59 of the 60 chickens were correctly partitioned. A sufficient number of HWLER cycles is needed to assure initial segregation of enough informative individuals of either breed that their complete separation follows, and by focusing on the problematic pair of breeds, that number of cycles is vastly reduced. Rosenberg et al. (2001) used STRUCTURE with numerous runs of the chicken data to test values for the number of sources between 1 and 23, determined that the best supported values were 17, 18, or 19, but allowed that small numbers of individuals were assigned to additional subsets if more than 19 were specified. Whereas HWLER separated all individuals of 18 of the 20 breeds into pure subsets, STRUCTURE and the algorithm used by Rosenberg et al. (2001) managed the same for only five breeds but also largely succeeded for 11 additional breeds.

For the Sashin Creek rainbow and steelhead trout data, several surprises in population structure were discovered. First, the rainbow trout sampled from the smaller Round Lake, which are progeny of a transplant 60 years earlier, were found to be composed of three populations, whereas those sampled from the larger, transplant source (Sashin Lake) were from a single population. Second, a population not sampled in the lakes may have been present (probability = 0.56) in middle Sashin Creek, which receives downstream survivors of falls in the outlet streams from the two lakes. Third and last, the estuary sample almost certainly (probability > 0.99) included steelhead from more than the single population expected and likely from as many as four such populations, in addition to populations represented by the samples from the lakes.

The possibility of hybrids among the rainbow trout populations in Round Lake concerned a reviewer, and so the samples were re-examined for hybrids using two programs. First, the program NewHybrids (http://ib.berkeley.edu/labs/slatkin/eriq/software/software.htm) implements a method specific for two populations and their hybrids (Anderson and Thompson 2002). Second, the program STRUCTURE implements a different method for any specified number of

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populations underlying hybrids (Pritchard et al. 2000; Falush et al. 2003). NewHybrids computed posterior probabilities for three categories of genotypes, F_1 hybrids, or purebreds of either of two populations. A total of 59 of 60 Round Lake individuals had been identified by HWLER as derived from either of two populations of assumed purebreds: 43 from the first population and 16 from the second one. NewHybrids was applied to the combined sample of 59 unlabeled individuals and confirmed the analysis by HWLER. The average posterior probabilities from NewHybrids for the aforementioned 43 unlabeled individuals equaled 0.97 (range 0.61–1.00); this indicated that they were purebreds from one population. For the other 16 unlabeled individuals, the corresponding average equaled 0.94 (range 0.64–1.00); this indicated that they were purebreds from a second population. STRUCTURE was applied three times to the 60 unlabeled Round Lake individuals with 1, 2, and 3 populations specified as present. Each time, a burn-in of 3 million samples for the unknowns was discarded and 1 million samples were kept for analysis. The posterior probabilities for number of populations present equaled 0.12, 0.87, and 0.01 for 1, 2, and 3 populations, respectively, thereby agreeing reasonably with HWLER. However, with two or three populations specified, every individual of the supposed purebred clusters previously identified by HWLER or NewHybrids was estimated by STRUCTURE to be a hybrid, with approximately equal contributions of allele copies from the populations it detected. Subsequently, when the unlabeled individuals of either of the two purported purebred clusters identified by HWLER or NewHybrids were analyzed separately with STRUCTURE, the posterior probability was nearly equal to 1 that single sources were present in both. A possible explanation for the inconsistent analyses from STRUCTURE is provided in the program user's manual (Pritchard and Wen 2003): "For some data sets there may be multiple modes, and the current implementation of *structure* does not normally cross between them in runs of realistic length. This means that different runs can produce substantially different answers, and longer runs will probably not fix this." Quite likely, alternating a split–merge sampler with its Gibbs sampler for hybrid analysis, both applied to allele copies, would improve STRUCTURE's performance. Of course, the better performance would cause label switching and necessitate its resolution.

The program HWLER can be used for at least two kinds of analyses, either population mixture analysis or baseline evaluation. For population mixture analysis, exploratory research programs, in which origins of individuals are highly uncertain, should benefit most from the open-ended Dirichlet process mixture model that allows for some or even all source populations to be missing from the baseline sampling. The number of exploratory applications must be vast. In contrast with Atlantic (*Salmo salar*) and Pacific salmon (*Oncorhynchus* spp.) that are currently common subjects, most species are difficult to sample as separate populations. Subsets of the partitions corresponding to extra-baseline populations will indicate their magnitudes and provide information about their genetic composition. Depending on the size of the extra-baseline contributions detected, further search for the separate breeding populations may be necessary. More mature research programs in which the populations present in mixtures are well known and routine sampling is used to assess their contributions can safely use the earlier likelihood or Bayesian methods based on the finite mixture model. However, the earlier methods may be less efficient by not requiring HWLE for the subsets of mixture individuals assigned to separate sources. Probably the most common research situations on population mixtures lie between these extremes, and the analyst would be advised to perform at least an occasional check for completeness of the current baseline by employing HWLER.

Genetic differences among baseline populations are commonly evaluated by simulation. Mixtures of any composition can be simulated from the baseline samples and the composition estimated by the maximum likelihood method using the programs SPAM (Debevec et al. 2000) or GMA (Kalinowski 2003). The empirical distributions of these composition estimates are useful for design of sampling programs (e.g., selection of loci and sample sizes). However, an acid test of a baseline is the separation of baseline individuals without use of their labels. This ultimate test is best performed with HWLER.

The construction of binary trees using the program ANALYSE was invaluable for interpretation of the partitions drawn by HWLER. The discovery during review that program ANALYSE is being superseded by the program PartitionView (http://www.univ-montp2.fr/~genetix/partition/partition.htm; Dawson and Belkhir 2001) is welcome news. PartitionView is based on a superior clustering algorithm that makes use of exact co-assignment probabilities for sets of any size (K. Dawson, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK, personal communication).

The program HWLER is demanding of computer time, yet almost certainly more efficient than either STRUCTURE or PARTITION. Given sufficient computing time, any of the three programs should generate equivalent posterior partition distributions for a mixture sample. With current desktop machines, such as the Intel Pentium III machine (Intel Corporation, Santa Clara, California) with processor speed of 800 MHz used here, processing of samples like those considered requires several hours to several days by HWLER. Speed of computation will continue to increase so that time will be less a hindrance and application of the program can become routine. In the meantime, the Fortran code of HWLER is being adapted for use on high-speed computers of the Arctic Region Supercomputing Center at the University of Alaska Fairbanks (Alaska, USA). Experiences using HWLER on such machines should prove beneficial to the fisheries and genetics communities involved in this fascinating intersection of technology and natural resource management.

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proved the final version of the manuscript. Use of trade names does not imply endorsement by the US government.

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Appendices A and B appear on the following pages.

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Appendix A. The Gibbs sampler with baseline samples.

Denote the fixed set of indices for baseline populations as $B = \{1,2,\ldots,|B|\}$, where the total number of baseline populations is $|B|$. Denote by $\boldsymbol{Y}_i = (\boldsymbol{y}_{i1}, \boldsymbol{y}_{i2}, \ldots, \boldsymbol{y}_{iL})$ the arrays of allele counts for L loci in the baseline sample for the ith population, and let $\boldsymbol{Y} = (\boldsymbol{Y}_1, \ldots, \boldsymbol{Y}_{|B|})$ denote the entire baseline collection of allele counts for the $|B|$ populations. A partition, $\boldsymbol{\eta} = (\boldsymbol{\eta}_B, \boldsymbol{\eta}_X)$, of the mixture sample individuals is a collection of $|\boldsymbol{\eta}|$ non-empty, exhaustive, and mutually exclusive HWLE subsets that purportedly were contributed by $|\boldsymbol{\eta}_B|$ baseline populations and $|\boldsymbol{\eta}_X|$ extra-baseline populations. For $S \in \boldsymbol{\eta}_B$, the corresponding baseline array among $\boldsymbol{Y}_1, \ldots, \boldsymbol{Y}_{|B|}$ will be denoted by $\boldsymbol{Y}^S$. The computations can be started by arbitrarily partitioning the mixture sample. Then a Gibbs scan of the mixture sample for individual $m = 1,\ldots,M$ comprises the following steps:

1. Remove the mth individual from the current partition $\boldsymbol{\eta}$ to obtain $\boldsymbol{\eta}^{-m}$ and let the number of non-empty partition subsets remaining be denoted by $|\boldsymbol{\eta}^{-m}|$.
2. For each of the $|\boldsymbol{\eta}^{-m}|$ subsets $S \in \boldsymbol{\eta}^{-m}$, compute the full conditional probability for $m \in S$ by $\Pr(m \in S \mid \boldsymbol{\eta}^{-m}, \boldsymbol{X}, \boldsymbol{Y}) = b \cdot |S| \cdot \int F(\boldsymbol{X}_m \mid \boldsymbol{Q})\, \mathrm{d}H_S(\boldsymbol{Q})$, where

$$\mathrm{d}H_S(\boldsymbol{Q}) = \prod_{h=1}^{L} \mathrm{Dirichlet}\left(\boldsymbol{q}_h; \beta_{h1} + d^S_{-m,h,1} + y^S_{h,1}, \ldots, \beta_{hJ_h} + d^S_{-m,h,J_h} + y^S_{h,J_h}\right) \text{ and}$$

$d^S_{-m,h,j}$ is the count of the jth allele at locus h among individuals in subset S excluding the mth individual, and $y^S_{h,j}$ is the count of the jth allele at locus h among individuals in the baseline sample corresponding to S. If S corresponds to one of the $|\boldsymbol{\eta}_X^{-m}|$ extra-baseline populations, $y^S_{h,j} = 0$, $j = 1,\ldots,J_h$, $h = 1,\ldots,L$.

3. For each of the $(|B| - |\boldsymbol{\eta}_B^{-m}| + 1)$ baseline populations missing from $\boldsymbol{\eta}^{-m}$, compute the full conditional probability that the mth individual is a new baseline singleton subset, $S = \{m\}$, as

$$\Pr(m \in S \mid \boldsymbol{\eta}^{-m}, \boldsymbol{X}, \boldsymbol{Y}) = b \cdot \left(\frac{\alpha}{|B| - |\boldsymbol{\eta}_B^{-m}| + 1}\right) \cdot \int F(\boldsymbol{X}_m \mid \boldsymbol{Q})\, \mathrm{d}H_S(\boldsymbol{Q})$$

where $\mathrm{d}H_S(\boldsymbol{Q})$ is given at Step 2, with $d^S_{-m,h,j} = 0$, $j = 1,\ldots,J_h$, $h = 1,\ldots,L$.

4. Compute the full conditional probability of a new extra-baseline singleton subset, $S = \{m\}$, as

$$\Pr(m \in S \mid \boldsymbol{\eta}^{-m}, \boldsymbol{X}, \boldsymbol{Y}) = b \cdot \left(\frac{\alpha}{|B| - |\boldsymbol{\eta}_B^{-m}| + 1}\right) \cdot \int F(\boldsymbol{X}_m \mid \boldsymbol{Q})\, \mathrm{d}G_0(\boldsymbol{Q})$$

5. Assign the mth individual randomly with the probabilities at Steps 2, 3, and 4.

The integral at Step 2 is $\int F(\boldsymbol{X}_m \mid \boldsymbol{Q})\, \mathrm{d}H_S(\boldsymbol{Q}) = \psi(\boldsymbol{X}_m, \boldsymbol{d}^S_{-m} + \boldsymbol{Y}^S, \boldsymbol{\beta})$, where the function ψ is defined in eq. 12, $\boldsymbol{d}^S_{-m} = (d^S_{-m,h,j}, h = 1,\ldots,L, j = 1,\ldots,J_h)$, and $\boldsymbol{Y}^S = (y^S_{h,j}, h = 1,\ldots,L, j = 1,\ldots,J_h)$. The integral at Step 3 is obtained from that at Step 2 by setting all $d^S_{-m,h,j} = 0$. The integral at Step 4 is obtained from that at Step 2 by setting all $d^S_{-m,h,j} = 0$ and $y^S_{h,j} = 0$. The scalar b normalizes the values at Steps 2, 3, and 4 so that the $(|B| + |\boldsymbol{\eta}_X^{-m}| + 1)$ full conditional probabilities sum to 1.

Appendix B. Sequentially allocated merge–split (SAMS) sampler with baseline samples.

The steps of the SAMS sampler with baseline samples available are as follows:

1. Draw a pair of individuals, i and j, at random without replacement from the mixture sample $\{1,\ldots,M\}$.
2. If i and j both belong to one of the subsets S of the partition $\boldsymbol{\eta} = (\boldsymbol{\eta}_B, \boldsymbol{\eta}_X)$, propose a split of S and the corresponding new partition $\boldsymbol{\eta}^{\mathrm{split}} = (\boldsymbol{\eta}_B^{\mathrm{split}}, \boldsymbol{\eta}_X^{\mathrm{split}})$ that has one more extra-baseline subset in $\boldsymbol{\eta}_X^{\mathrm{split}}$ than $\boldsymbol{\eta}_X$ does. If $S \in \boldsymbol{\eta}_X$, the split proceeds as if no baseline was available. If $S \in \boldsymbol{\eta}_B$, then select either individual i or j at random with equal probability to remain with the baseline population.
   (*a*) Begin the split by removing individuals i and j from S and form the singleton sets, $S_i = \{i\}$ and $S_j = \{j\}$.
   (*b*) Randomly permute the list of the individuals remaining in S and let k index their order in the permuted list.
   (*c*) Suppose individual i remains associated with the individuals of the baseline population; then individual k is added to $S_i \in \boldsymbol{\eta}_B^{\mathrm{split}}$ with probability that incorporates the associated baseline allele counts:

$$\Pr(k \in S_i \mid S_{i,<k}, S_{j,<k}, \boldsymbol{X}, \boldsymbol{Y}^S) = \frac{|S_{i,<k}| \cdot P(\boldsymbol{X}_k \mid S_{i,<k}, \boldsymbol{Y}^S)}{|S_{i,<k}| \cdot P(\boldsymbol{X}_k \mid S_{i,<k}, \boldsymbol{Y}^S) + |S_{j,<k}| \cdot P(\boldsymbol{X}_k \mid S_{j,<k})}$$

where

$$P(\boldsymbol{X}_k \mid S_{i,<k}, \boldsymbol{Y}^S) = \psi(\boldsymbol{X}_k, \boldsymbol{d}^{S_{i,<k}} + \boldsymbol{Y}^S, \boldsymbol{\beta})$$

and

$$\boldsymbol{d}^{S_{i,<k}} = (d^{S_{i,<k}}_{h,j}, h = 1,\ldots,L, j = 1,\ldots,J_h)$$

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are the allele counts among individuals preceding the kth individual assigned to the baseline population. Otherwise add individual k to $S_j \in \boldsymbol{\eta}_B^{split}$.

(*d*) Accept the proposed split with probability equal to the Metropolis–Hastings ratio. The ratio incorporates the total count of alleles among individuals of the baseline population and is the product of three individual ratios, viz.

$$\alpha(\boldsymbol{\eta}^{split} | \boldsymbol{\eta}, \boldsymbol{Y}^S) = \min\left[1, \frac{\rho(\boldsymbol{\eta} | \boldsymbol{\eta}^{split})}{\rho(\boldsymbol{\eta}^{split} | \boldsymbol{\eta}, \boldsymbol{Y}^S)} \cdot \frac{P(\boldsymbol{\eta}^{split})}{P(\boldsymbol{\eta})} \cdot \frac{L(\boldsymbol{\eta}^{split} | \boldsymbol{X}, \boldsymbol{Y}^S)}{L(\boldsymbol{\eta} | \boldsymbol{X}, \boldsymbol{Y}^S)}\right]$$

where

$$\frac{\rho(\boldsymbol{\eta} | \boldsymbol{\eta}^{split})}{\rho(\boldsymbol{\eta}^{split} | \boldsymbol{\eta}, \boldsymbol{Y}^S)} = \frac{1}{\prod_{k:z_k=i} \Pr(k \in S_i | S_{i,<k}, S_{j,<k}, \boldsymbol{X}, \boldsymbol{Y}^S) \cdot \prod_{k:z_k=j} \Pr(k \in S_j | S_{i,<k}, S_{j,<k}, \boldsymbol{X})}$$

$\frac{P(\boldsymbol{\eta}^{split})}{P(\boldsymbol{\eta})}$ is defined in eq. 15 and

$$\frac{L(\boldsymbol{\eta}^{split} | \boldsymbol{X}, \boldsymbol{Y}^S)}{L(\boldsymbol{\eta} | \boldsymbol{X}, \boldsymbol{Y}^S)} = \frac{\prod_{k \in S_i} P(\boldsymbol{X}_k | S_{i,<k}, \boldsymbol{Y}^S) \cdot \prod_{k \in S_j} P(\boldsymbol{X}_k | S_{j,<k})}{\prod_{k \in S} P(\boldsymbol{X}_k | S_{<k}, \boldsymbol{Y}^S)}$$

3. If i and j belong to different subsets of the partition $\boldsymbol{\eta}$, propose to merge the individuals in the same subsets as i and j, say S_i and S_j, respectively, to form the merged set $S = S_i \cup S_j$ and the partition $\boldsymbol{\eta}^{merge}$ that has one fewer subsets than $\boldsymbol{\eta}$. None, one, or both S_i and S_j may be in $\boldsymbol{\eta}_B$.

(*a*) Suppose neither S_i nor S_j belongs to $\boldsymbol{\eta}_B$. Then the merged set $S \in \boldsymbol{\eta}_A^{merge}$ and the merge procedure is the same as if no baseline was available.

(*b*) Suppose both S_i and S_j belong to $\boldsymbol{\eta}_B$ and that $|S_i| \geq |S_j|$. Then the merged set $S \in \boldsymbol{\eta}_B^{merge}$ is proposed with its associated baseline population being the same as that of individual i. Compute the Metropolis–Hastings ratio and accept the merge proposal with probability given by a modified ratio that incorporates the allele counts among individuals of the associated baseline samples, $\boldsymbol{Y}^{S_i}$ and $\boldsymbol{Y}^{S_j}$. The Metropolis–Hastings ratio is a product of three individual ratios, viz.

$$\alpha(\boldsymbol{\eta}^{merge} | \boldsymbol{\eta}, \boldsymbol{Y}^{S_i}, \boldsymbol{Y}^{S_j}) = \min\left[1, \frac{\rho(\boldsymbol{\eta} | \boldsymbol{\eta}^{merge}, \boldsymbol{Y}^{S_i}, \boldsymbol{Y}^{S_j})}{\rho(\boldsymbol{\eta}^{merge} | \boldsymbol{\eta})} \cdot \frac{P(\boldsymbol{\eta}^{merge})}{P(\boldsymbol{\eta})} \cdot \frac{L(\boldsymbol{\eta}^{merge} | \boldsymbol{X}, \boldsymbol{Y}^{S_i})}{L(\boldsymbol{\eta} | \boldsymbol{X}, \boldsymbol{Y}^{S_i}, \boldsymbol{Y}^{S_j})}\right]$$

where

$$\frac{\rho(\boldsymbol{\eta} | \boldsymbol{\eta}^{merge}, \boldsymbol{Y}^{S_i}, \boldsymbol{Y}^{S_j})}{\rho(\boldsymbol{\eta}^{merge} | \boldsymbol{\eta})} = \prod_{k:z_k=i} \Pr(k \in S_i | S_{i,<k}, S_{j,<k}, \boldsymbol{X}, \boldsymbol{Y}^{S_i}) \cdot \prod_{k:z_k=j} \Pr(k \in S_j | S_{i,<k}, S_{j,<k}, \boldsymbol{X}, \boldsymbol{Y}^{S_j})$$

$\frac{P(\boldsymbol{\eta}^{merge})}{P(\boldsymbol{\eta})}$ is defined in eq. 16, and

$$\frac{L(\boldsymbol{\eta}^{merge} | \boldsymbol{X}, \boldsymbol{Y}^{S_i})}{L(\boldsymbol{\eta} | \boldsymbol{X}, \boldsymbol{Y}^{S_i}, \boldsymbol{Y}^{S_j})} = \frac{\prod_{k \in S} P(\boldsymbol{X}_k | S_{<k}, \boldsymbol{Y}^{S_i})}{\prod_{k \in S_i} P(\boldsymbol{X}_k | S_{i,<k}, \boldsymbol{Y}^{S_i}) \cdot \prod_{k \in S_j} P(\boldsymbol{X}_k | S_{j,<k}, \boldsymbol{Y}^{S_j})}$$

If the merge is accepted, the merged subset S is assigned to the baseline population of individual i.

(*c*) If only one of the subsets S_i and S_j is of a baseline population, say S_j, then the computations of step 3*b* omit the allele counts $\boldsymbol{Y}^{S_j}$, and if the merge is accepted, the merged set S is associated with the baseline population of individual i.

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Mechanisms of density dependence in stream fish: exploitation competition for food reduces growth of adult European bullheads (*Cottus gobio*)

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Abstract: In field experiments using cage enclosures, exploitation competition for invertebrate prey reduced individual growth of adult European bullheads (*Cottus gobio*) despite a dietary shift that maintained total prey biomass consumption. Growth of bullheads was negatively density dependent over a range of densities found in the field and total biomass production per enclosure was unrelated to stocking density. Individuals grew faster when invertebrate densities were experimentally elevated above ambient levels, indicating that bullheads were food limited. Parallel dietary shifts in response to manipulation of both bullhead density and resource availability suggested that exploitation competition for preferred *Gammarus pulex* prey was the primary cause of density-dependent growth. Switching to smaller prey species did not prevent growth of bullheads declining with increasing per capita food competition, indicating that the alternative prey were less profitable. Evidence for interference competition was limited. These results caution against the assumption that demographic rates of stream fish are density independent after the juvenile phase and demonstrate instead that density-dependent growth may potentially regulate populations at the adult stage via effects on fecundity and survival.

Résumé : Dans des expériences de terrain dans des enclos en forme de cages, la compétition d'exploitation pour les proies invertébrées a réduit la croissance individuelle de goujons (*Cottus gobio*) malgré un changement de régime alimentaire qui a permis le maintien de la consommation totale de proies en biomasse. La croissance des goujons est reliée négativement à la densité dans la gamme des densités observées en nature et la biomasse totale produite par enclos est indépendante de la densité de l'empoissonnement. Les individus croissent plus rapidement lorsque les densités d'invertébrés sont accrues expérimentalement au-dessus des densités ambiantes, ce qui indique que les goujons sont limités par la nourriture. Des changements de régime alimentaire menés en parallèle en réaction à la manipulation à la fois de la densité des goujons et de la disponibilité des ressources laissent croire que la compétition d'exploitation pour la proie préférée *Gammarus pulex* est la cause principale de la dépendance de la croissance vis à vis la densité. La substitution d'espèces de proies plus petites n'empêche pas le déclin de la croissance des goujons en fonction de l'augmentation de la compétition pour la nourriture par individu, ce qui indique que les proies de rechange sont moins profitables. Il y a peu d'indications de l'existence d'une compétition d'interférence. Ces résultats mettent en garde contre la présupposition que les taux démographiques des poissons d'eau courante sont indépendants de la densité une fois la phase juvénile terminée et démontrent, au contraire, qu'une croissance dépendante de la densité peut potentiellement contrôler les populations au stade adulte par l'intermédiaire des effets sur la fécondité et la survie.

[Traduit par la Rédaction]

Introduction

Determining the mechanisms by which populations are regulated has long been a core theme in animal ecology (Nicholson 1933; Andrewartha and Birch 1954; Turchin 1999). The long-term persistence of populations without extinction suggests that regulation should be ubiquitous in nature, yet measuring density dependence in the field has proved challenging (Wolda and Dennis 1993; Murdoch 1994; Rose et al. 2001). In particular, there is an need to better understand the underlying biological mechanisms, specifically the processes that produce density dependence and the stage in the life cycle at which they occur (Sinclair 1989; Murdoch 1994; Rose et al. 2001). Field manipulations of population density

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offer a direct approach to examining density dependence in demographic rates but often pose substantial practical difficulties and consequently are seldom performed in many systems (Harrison and Cappuccino 1995).

Density-dependent mortality during the juvenile (prerecruit) stage is believed to be the primary mechanism regulating fish populations (Sinclair 1989; Shepherd and Cushing 1990). Individual-based modelling of prey consumption predicts that competition among members of a cohort will result in density-dependent individual growth and mortality at a critical body mass corresponding to the late-larval or juvenile life stage (Cowan et al. 2000). For stream fish, the majority of field studies confirm that density-dependent mortality occurs primarily at the larval or early juvenile stage (Le Cren 1973; Mortensen 1977; Grenouillet et al. 2001) and that mortality is density independent thereafter (Elliott 1985; Jonsson et al. 1998; Cattaneo et al. 2002). It has been suggested, however, that populations could also be regulated at the adult stage via density dependence in individual growth rate (Shepherd and Cushing 1990). This mechanism is potentially very powerful in its effects because fecundity and survival are strongly correlated with body size in fish (Lorenzen 1996; Sogard 1997; Rose et al. 2001). But while this phenomenon is well documented in lacustrine fish populations (Lorenzen and Enberg 2002), empirical evidence for density dependence in adult stream fish is extremely limited. Elliott and Hurley (1998) found that resident brown trout (*Salmo trutta*) in a Lake District stream were regulated at the adult stage but could not establish the cause, while Jenkins et al. (1999) and Bohlin et al. (2002) reported that individual growth of >0+ brown trout declined with population density.

Food and foraging space are commonly cited as potential limiting factors for stream fish. Density-dependent mortality in juveniles is thought to involve an interaction between food supply and predation whereby exploitation for food at high densities results in slower growth and prolongs the critical period during which fish are vulnerable to gape-limited predators (Sinclair 1989; Shepherd and Cushing 1990). However, we are not aware of any empirical studies that support this hypothesis. In salmonids, interference competition for territories has been shown to regulate populations via density-dependent mortality and emigration (Elliott 1985, 1990; Grant and Kramer 1990), although strong compensatory growth responses at low population densities suggest that exploitation competition may also be important (Jenkins et al. 1999). Stream fish can significantly reduce densities of invertebrate prey through predation (for reviews, see Wooster 1994; Dahl and Greenberg 1996; Shurin et al. 2002), but there is little evidence that strong top-down effects can result in exploitation competition among predators. Experimental manipulation of resource availability (Keeley 2001; Boss and Richardson 2002) and direct interaction with conspecifics (Imre et al. 2002) holds much potential to distinguish alternative competitive mechanisms, but to our knowledge, such manipulations have not been performed simultaneously to date.

The aim of this study was to uncover the mechanisms that give rise to density dependence in a small benthic fish, the European bullhead (*Cottus gobio*). Bullheads show high site fidelity, have low movement rates (Smyly 1957; Downhower et al. 1990), and can attain high densities in shallow stony streams. These characteristics make them ideal for investigating population-level processes by experimental manipulation. Bullheads are abundant in the chalk streams of southern England (Mann 1971), yet the factors controlling their population size are not well understood. Early life stages (eggs and fry) can suffer high mortality owing to invertebrate predation and fungal infection (Green 1975; Fox 1978), and there is some evidence to suggest that growth of fish may be reduced at high densities (Fox 1978; Edwards and Brooker 1982). As visual ambush predators, bullheads positively select large, active invertebrates such as *Gammarus pulex* (Smyly 1957; Welton et al. 1983) and can significantly reduce local densities of key prey species (Englund and Olsson 1996; Dahl 1998). In addition, adult fish behave agonistically towards conspecifics when feeding and are territorial, particularly during the breeding season (Smyly 1957; Ladich 1989). Thus, both exploitation and interference competition could potentially cause density-dependent individual growth at the adult stage. We tested this hypothesis by conducting two manipulative field experiments in situ using cage enclosures. The first tested for density dependence by examining the effect of fish density on growth in body size, prey consumption, and total food intake. The second experiment held fish density constant while manipulating food availability and the level of contact with conspecifics to evaluate the relative influence of exploitation and interference competition.

Materials and methods

Study site

We conducted our experiments in the Brandy Stream, a side channel of the River Itchen in southern England (51°03′N, 1°19′W; altitude 30 m). The Itchen is typical of the chalk streams of southern and eastern England, being fed by ground water from Cretaceous chalk aquifers and characterized by high thermal and hydrological stability and high primary productivity. Mean water temperature during experiments 1 and 2 was 15.5 °C (minimum 13.7 °C, maximum 17.6 °C) and 12.2 °C (minimum 10.8 °C, maximum 14.1 °C), respectively. At the study site, the stream averages 5.3 m in width and is generally shallow (<0.30 m) and swift flowing (>0.15 $m \cdot s^{-1}$), with a substrate of flint gravel and cobbles. An electrofishing survey during August 2002 estimated the density of adult bullheads at 3.4 $fish \cdot m^{-2}$ in the stream as a whole and 7.6 $fish \cdot m^{-2}$ in preferred riffle habitats (Davey et al. 2005).

Experimental enclosures

We performed the experimental manipulations using cage enclosures, each 1.4 m long, 0.8 m wide (enclosed area = 1.12 m^2), and 0.3 m high. Enclosures had solid metal sides and base and 6 mm wire mesh on the upstream and downstream ends to permit water to flow through and invertebrates to drift freely in and out. Enclosures were arranged at 1–2 m intervals in rows of two or three across the stream, with the rows spaced 4–5 m apart. Enclosures in neighbouring rows were staggered to minimize possible shadow effects. Enclosures were established in water 0.17–0.27 m deep with velocities of 0.17–0.39 $m \cdot s^{-1}$. The base of each enclo-

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sure was then covered with 10–20 mm gravel, creating a substrate 25 mm deep, and bricks and cobbles placed on top to provide shelter and mimic a riffle habitat. Plastic netting was placed over the open top of each enclosure to deter avian predators. A coarse mesh was used that had a negligible shading effect. Although the exclusion of predators has the potential to affect the behaviour of the fish, this was necessary to ensure that the treatments were maintained. The upstream and downstream wire meshes were removed for 6 weeks prior to the start of each experiment to allow invertebrate prey to colonize the enclosures. Comparison of samples collected from the downstream ends of four enclosures at the start of experiment 2 with four samples from an adjacent riffle indicated that densities of *G. pulex* tended to be higher inside the enclosures (mean ± SE: 4142 ± 1011 individuals·m^{-2}) than outside (2456 ± 305 individuals·m^{-2}) but that total macroinvertebrate densities were comparable (24 128 ± 2307 individuals·m^{-2} inside, 22 081 ± 1308 individuals·m^{-2} outside). One-way analysis of variance (ANOVA) was nonsignificant in both cases ($P > 0.05$), although statistical power was low. Once replaced to enclose fish, the wire meshes were cleaned every 12 h to remove accumulated plant debris and maintain water flow through the enclosures. During each experiment, water depth and water velocity were measured inside each enclosure to check that there were no differences in physical conditions among treatments.

Experiment 1: testing for density dependence

Twelve replicate enclosures were established on 7 June 2000 as described above. All fish used in the experiment were collected locally from the Brandy Stream by electrofishing between 20 and 22 July and held in stock enclosures. On 23 July, 56 adult bullheads were weighed to the nearest 0.01 g using an electronic balance and measured to the nearest 0.1 mm (total length (TL)) using callipers. In each case, two replicate measurements were taken for each individual and averaged to give a single data point. Fish were randomly allocated to three density treatments: two, four, and eight fish per enclosure. These densities of 1.8, 3.6, and 7.1 fish·m^{-2} corresponded to approximately half, equal to, and double the mean density of adult bullheads in the Brandy Stream and are within the range of densities observed in preferred riffle habitats (Davey et al. 2005). The experimental animals ranged in initial mass from 2.05 to 7.38 g (mean 3.56 g) and in initial TL from 55.7 to 82.3 mm (mean 65.5 mm). Treatments were replicated four times and randomly assigned to enclosures. One-way ANOVA showed no significant relationship between stocking density and either water depth, water velocity, or mean fish mass (all $P > 0.10$). Fish were held in the enclosures for 14 days. Three bullheads died during the experiment: two fish died in the four-fish treatment, one on 26 and one on 27 July, and one fish died in the eight-fish treatment on 30 July. Dead bullheads were replaced with fish of similar size to maintain the treatments.

Experiment 2: distinguishing between exploitation and interference competition

For the second experiment, we used a factorial experimental design, crossing two levels of food availability with two levels of isolation (Fig. 1). By simultaneously manipulating both resource availability and the amount of direct interaction between conspecifics, we were able to determine whether density-dependent rates of prey consumption and food intake by bullheads, and hence individual growth, were caused directly by interference competition and (or) mediated by changes in prey density (exploitation competition).

An array of 20 enclosures was established in the stream on 14 August 2002. We supplemented food availability in half of the enclosures by periodically adding benthic macroinvertebrates during the experiment to elevate prey densities (see below). Prey densities in the control treatment were left at ambient levels. To manipulate the degree of isolation, we erected two barriers in each enclosure parallel to the water flow, so partitioning the space into three sections of equal area. To erect the barriers securely, the downstream meshes were moved to the centre of the enclosures. Consequently, the enclosed area was half of that in experiment 1 (0.56 m^2). The barriers were constructed from 6 mm wire mesh that was permeable to invertebrate prey. To restrict interaction between bullheads, half of the enclosures were fitted with complete barriers that prevented fish moving between sections and fish stocked individually into each section. Installing barriers to isolate fish individually allowed us to evaluate the effect of interference competition by providing a measure of the performance of bullheads in the absence of direct interactions between conspecifics. Control enclosures were fitted with partial barriers containing a 0.3 m gap that allowed fish to move between sections and interact normally. Each of the four treatments was replicated five times and treatments were randomly assigned to enclosures.

All experimental fish were sourced from the Brandy Stream by electrofishing on 27 September 2002 and held in stock enclosures. On 29 September, 60 adult bullheads were weighed to the nearest 0.01 g and measured to the nearest 0.1 mm (TL); three replicate measurements were taken for each individual and averaged to give a single data point. Fish ranged in initial mass from 1.47 to 4.52 g (mean 2.56 g) and in initial TL from 52.0 to 72.1 mm (mean 60.0 mm). Bullheads were marked with subcutaneous elastomer tags (Northwest Marine Technology Inc., Shaw Island, Washington) to allow individual recognition and randomly assigned to treatments. Three fish were released into each enclosure, one in the centre of each section, representing a density of 5.4 fish·m^{-2}. Two-way ANOVA of water depth, water velocity, and mean fish mass showed that there were no significant differences among treatments (all $P > 0.05$). The experiment was run for 12 days.

Macroinvertebrates were added to food addition treatments on 2, 6, and 9 October. All animals were collected from the Brandy Stream by carefully disturbing the streambed and catching downstream-drifting individuals in a pond net (500 µm mesh). To control the number of animals added, replicate 30 mL samples of macroinvertebrates were measured out using a measuring cylinder. On each date, a total of 90 mL of macroinvertebrates were released into each food addition enclosure, 30 mL·section^{-1}. Analysis of samples ($n = 5$) showed that *G. pulex* accounted for 90% of all animals, with a mean of 1645 (±298 SD) individuals·90 mL^{-1}. This was equivalent to elevating benthic densities of *G. pulex* by an average of 8812 individuals·m^{-2} during the course of the experiment, approximately tripling the ambient density. To reduce the immediate downstream drift of animals, a board was temporarily positioned across the up-

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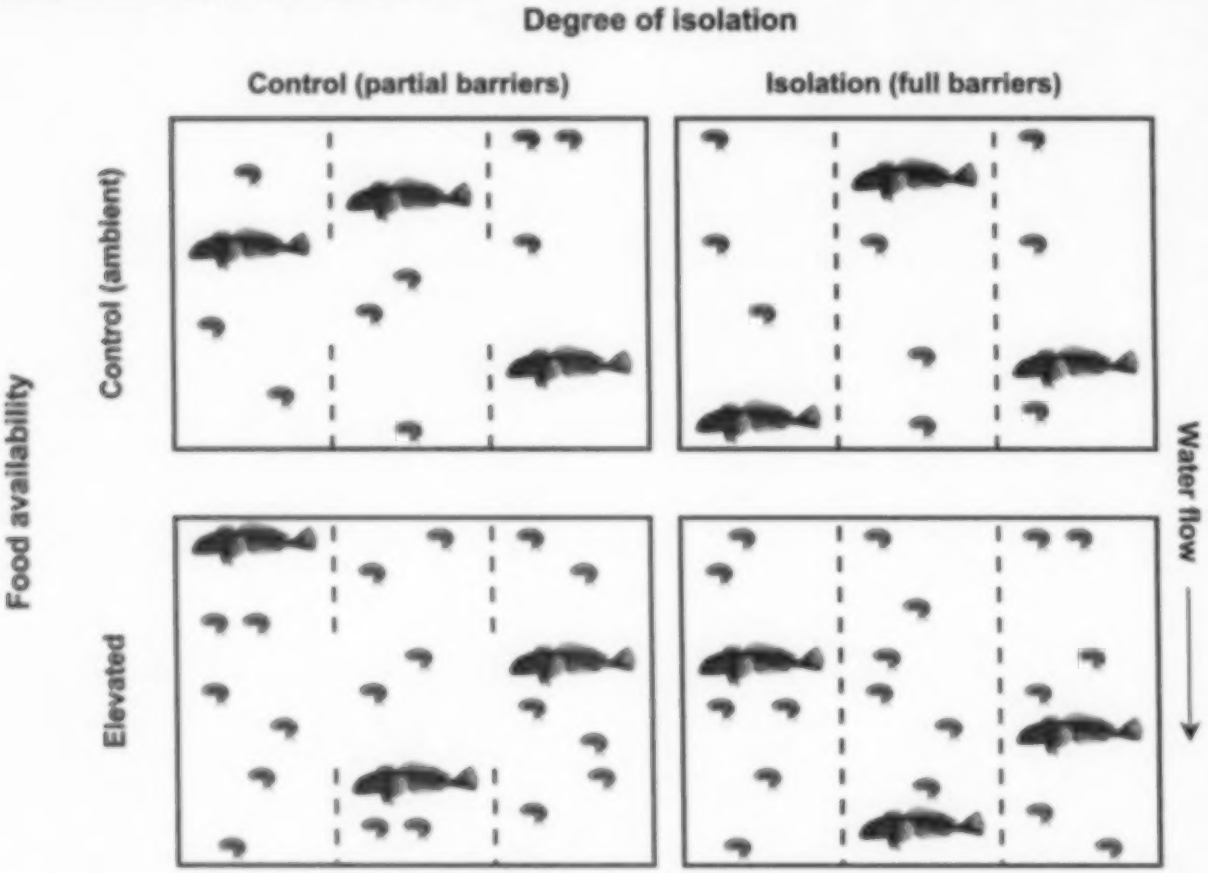
Fig. 1. Experimental design to evaluate the relative influence of exploitation and interference competition. Bullheads (*Cottus gobio*) were held in replicate stream enclosures under two levels of prey density (ambient and elevated), both with and without longitudinal barriers (broken lines) physically isolating conspecifics.



stream mouth of recipient enclosures to stop water flow and the macroinvertebrates then released as close to the substrate as possible. As a procedural control, the remaining 10 cages were also temporarily screened off and 90 mL of gravel added to each to simulate the disturbance caused by adding invertebrates.

Data collection

At the end of each experiment, the enclosures were searched and bullheads removed with a dip net. Fish were then killed by an overdose of anaesthetic, identified, reweighed, and remeasured as at the start of the experiment and preserved in 70% ethanol solution. This work was conducted between 0700 and 1000 to minimize digestion of consumed prey. In the laboratory, the stomachs of experimental fish were dissected out and their contents examined under 40× magnification using a dissecting microscope. Prey items were identified to the lowest practical taxonomic level, counted, and measured to the nearest 0.01 mm using a graticule. Dimensions of prey items were converted to dry weight biomass using published mass–length relationships (Ladle et al. 1972; Bass 1976; Mackey 1977; Mason 1977; Welton 1979; Meyer 1989). The preservation method and prey type in published equations were matched as closely as possible to those used in the present study to maximize the accuracy of estimates. Stomach contents were observed in various degrees of digestion. Incomplete prey items were assumed to be whole for the purpose of biomass determination. Where no body dimension could be recorded, a biomass was attributed based on the average of other specimens within the sample. Occasionally, prey could not be identified and these were excluded from analysis.

Statistical analysis

The performance of bullheads was assessed by measuring growth in body size, prey consumption, and total food intake. Growth was expressed as the change over time in body mass and TL. Prey consumption was calculated as the number of individuals of each invertebrate taxon per fish stomach. Total food intake was measured as the total dry weight biomass of all prey consumed divided by fish mass to the power of 0.75 to account for the allometric relationship between body size and food consumption (Steingrimsson and Grant 1999). Two further metrics were calculated to test sub-

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sidiary hypotheses. To investigate the relationship between fish density and biomass production in experiment 1, production was calculated for each enclosure as the total change in body mass of all fish ($g \cdot m^{-2}$). To test the hypothesis that competition may increase variation in growth among individuals, the standard deviation of individual growth was calculated for each enclosure in experiment 2. Calculations were performed for surviving fish only. As mortality was low and unrelated to treatment in both experiments, this did not bias the results. In experiment 2, four fish that breached the barriers, and the four neighbours that they invaded, were omitted from the analysis.

Analyses were performed on the means for each enclosure ($n = 12$ data points for experiment 1 and $n = 20$ for experiment 2). Response variables from experiment 1 were regressed against fish density. Response variables were tested with Cochran's C test for homogeneity of variances (Cochran 1951). Growth in body mass, growth in TL, and consumption of simuliid larvae were $\log(x + 1)$ transformed to normalize the data and stabilize variances, while consumption of chironomid larvae could not be transformed and was instead analysed by Spearman's rank correlation. Response variables from experiment 2 were analysed using two-way ANOVA, with food availability, isolation, and their interaction as fixed factors. Growth in TL and simuliid consumption were again $\log(x + 1)$ transformed to correct heterogeneous variances. SPSS v.10.0 (SPSS Inc., Chicago, Illinois) and Statistica v.6.1 (Statsoft Inc., Tulsa, Oklahoma) were used for all statistical procedures and significance evaluated using $\alpha = 0.05$.

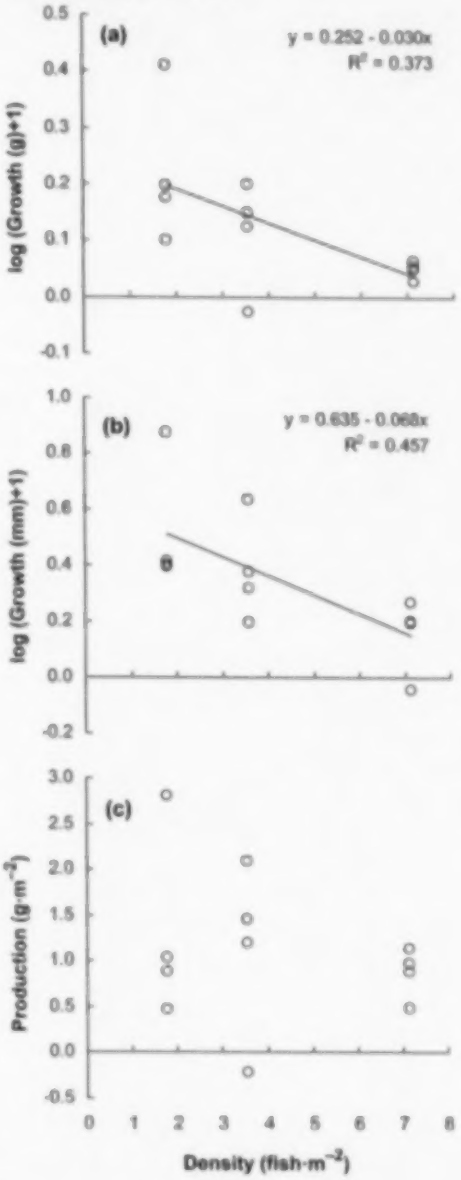
Results

Experiment 1: testing for density dependence

Fish density strongly affected bullhead performance. Both growth in mass (regression: $F_{[1,10]} = 5.95$, $P = 0.035$) (Fig. 2*a*) and growth in TL (regression: $F_{[1,10]} = 8.42$, $P = 0.016$) (Fig. 2*b*) were negatively density dependent. Mean growth in the highest-density treatment (0.12 g and 0.5 mm) was 83% lower than in the low-density control (0.73 g and 2.8 mm). As a result of strong density-dependent growth, total biomass production per enclosure was unrelated to stocking density (regression: $F_{[1,10]} = 0.58$, $P = 0.46$) (Fig. 2*c*).

The diet of bullheads was dominated numerically by *G. pulex* (67%) followed by *Baetis* nymphs (14%), simuliid larvae (11%), and chironomid larvae (4%). Consumption of chironomid larvae (Spearman's $r_s = 0.70$, $P = 0.011$, $n = 12$) and *Baetis* nymphs (regression: $F_{[1,10]} = 5.54$, $P = 0.040$) increased with bullhead density (Figs. 3*b* and 3*d*). In contrast, there was a suggestion that numbers of *G. pulex* consumed were lower at high densities (regression: $F_{[1,10]} = 4.33$, $P = 0.064$) (Fig. 3*a*), while consumption of simuliid larvae was unrelated to stocking density (regression: $F_{[1,10]} = 1.58$, $P = 0.24$) (Fig. 3*c*). Other prey taxa were consumed too infrequently for analysis. Mean prey biomass per fish was 24.9 mg dry weight and *G. pulex* accounted for over 94% of total prey biomass in all three treatments. There was a tendency for total prey biomass consumed per fish to decline with increasing fish density, but this effect was not statistically significant (regression: $F_{[1,10]} = 1.71$, $P = 0.22$).

Fig. 2. Mean individual growth of bullheads (*Cottus gobio*) in (*a*) mass and (*b*) total length and (*c*) total biomass production relative to fish density in cage enclosures. Data points are based on two, four, or eight fish per enclosure. Regression lines show significant relationships ($P < 0.05$).



Experiment 2: distinguishing between exploitation and interference competition

Mean growth in mass of bullheads was 97% higher in the food addition enclosures than in the controls (ANOVA: $F_{[1,16]} = 4.96$, $P = 0.041$) (Fig. 4*a*). Likewise, growth in TL tended to be greater in the food addition treatment, although this effect was marginally nonsignificant (ANOVA: $F_{[1,16]} =$

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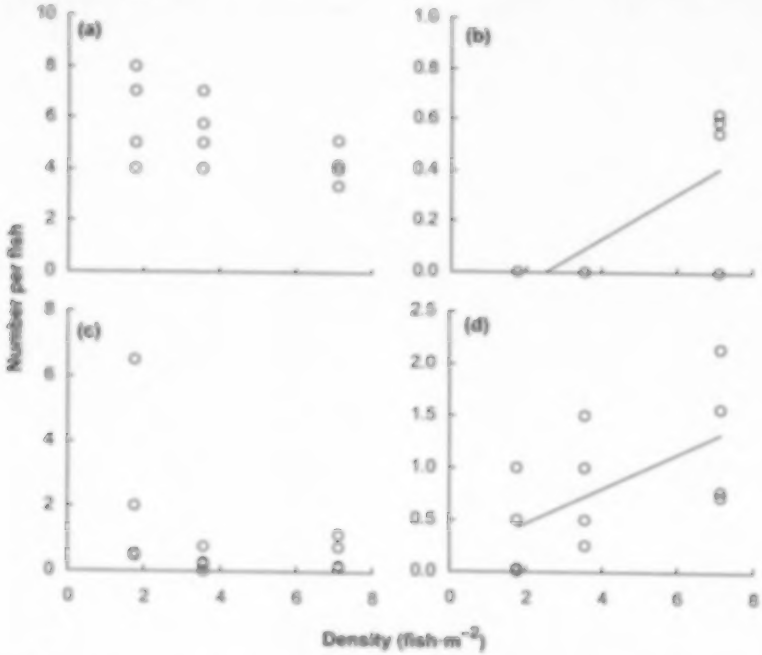
Fig. 3. Mean consumption of (*a*) *Gammarus pulex*, (*b*) chironomid larvae, (*c*) simuliid larvae, and (*d*) *Baetis* nymphs per bullhead (*Cottus gobio*) relative to fish density in cage enclosures. Data points are means based on two, four, or eight fish per enclosure. Lines show significant relationships ($P < 0.05$).



3.67, $P = 0.073$) (Fig. 4*b*). In contrast, isolation had no effect on growth in mass (ANOVA: $F_{[1,16]} = 0.33$, $P = 0.57$) or on growth in TL (ANOVA: $F_{[1,16]} = 0.06$, $P = 0.81$). The effect of food addition on growth did not depend on the level of isolation (ANOVA interaction: mass: $F_{[1,16]} = 0.82$, $P = 0.38$; TL: $F_{[1,16]} = 0.89$, $P = 0.36$) (Fig. 4). Within-enclosure variation in individual growth was unrelated to food availability, isolation, and their interaction for both growth in mass and growth in TL (ANOVA: all $P > 0.05$).

As in experiment 1, the diet of bullheads was numerically dominated by *G. pulex*, *Baetis* nymphs, simuliid larvae, and chironomid larvae (93% of all prey items). Bullheads displayed a strong dietary shift in response to food addition, consuming more *G. pulex* (ANOVA: $F_{[1,16]} = 9.53$, $P = 0.007$) (Fig. 5*a*), fewer chironomid larvae (ANOVA: $F_{[1,16]} = 5.57$, $P = 0.031$) (Fig. 5*b*), and fewer simuliid larvae (ANOVA: $F_{[1,16]} = 14.28$, $P = 0.002$) (Fig. 5*c*) at elevated prey densities. There was also a suggestion that consumption of *Baetis* nymphs was lower in food addition treatments (ANOVA: $F_{[1,16]} = 3.78$, $P = 0.070$) (Fig. 5*d*). Predation upon chironomid larvae (ANOVA: $F_{[1,16]} = 5.32$, $P = 0.035$) (Fig. 5*b*) and simuliid larvae (ANOVA: $F_{[1,16]} = 5.38$, $P = 0.034$) (Fig. 5*c*) was further reduced when fish were isolated by barriers. Consumption of *G. pulex* and *Baetis* nymphs was unaffected by the degree of isolation (ANOVA: $F_{[1,16]} = 0.16$, $P = 0.70$ and $F_{[1,16]} = 0.98$, $P = 0.34$, respectively) (Fig. 5). Interaction between food availability and isolation had no significant effect on consumption of any prey taxa (ANOVA: all $P > 0.20$). Bullheads contained a mean of 4.7 mg dry weight of invertebrate prey, and as in experiment 1, *G. pulex* accounted for the majority of prey biomass (64%). Total prey consumption was unaffected by food availability (ANOVA: $F_{[1,16]} = 0.73$, $P = 0.41$), isolation (ANOVA: $F_{[1,16]} = 0.01$, $P = 0.93$), or their interaction (ANOVA: $F_{[1,16]} = 1.03$, $P = 0.33$) (Fig. 6).

Discussion

The use of field enclosures to manipulate animal densities in situ risks altering the behaviour or habitat of the focal species. However, the small home ranges (Downhower et al. 1990) and high site fidelity of bullheads (Smyly 1957) suggest that the size of the enclosures would not have restricted their movement significantly over the time frame of the experiments. Indeed, the growth rates and dietary composition of bullheads during the experiments were comparable with those of previous studies of free-ranging fish in other chalk streams (Mann and Orr 1969; Mann 1971; Green 1975). Furthermore, the enclosures closely approximated natural conditions and supported an assemblage of invertebrate species similar to that in the surrounding stream. It seems unlikely, therefore, that the fish were stressed by confinement within enclosures or that the observed responses of bullheads were artefacts caused by the use of enclosures.

The growth rate of adult bullheads in enclosures was negatively density dependent over the range of densities observed in riffles in the field. The results confirm correlative evidence of density-dependent growth of bullheads in the field (Edwards and Brooker 1982) and support earlier suggestions that this might occur during the adult stage (Fox 1978). However, the results contrast with the prevailing view that density dependence occurs in stream fish almost exclusively at the larval or early juvenile stage (Sinclair 1989; Cowan et al. 2000) and add to a small but growing body of

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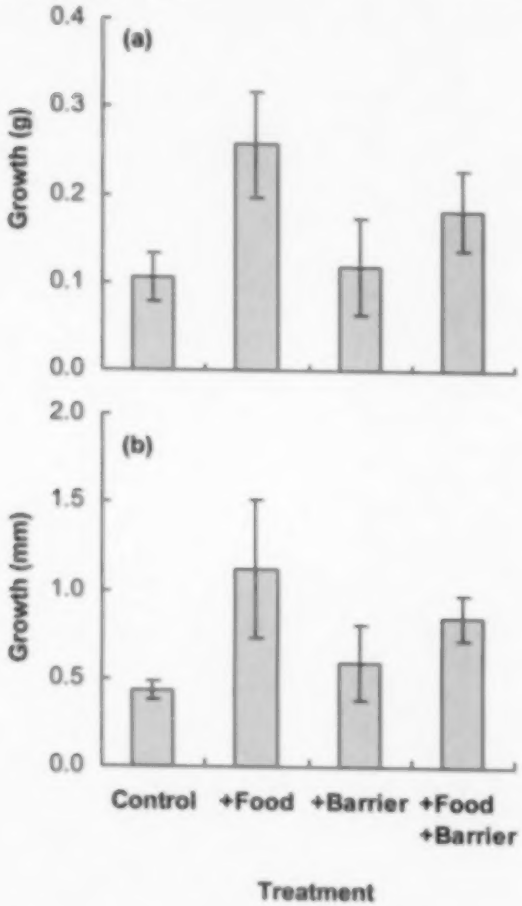
Fig. 4. Mean growth in (*a*) mass and (*b*) total length of bullheads (*Cottus gobio*) in cage enclosures. Fish were exposed to two levels of food availability (ambient and elevated), both with and without barriers physically isolating conspecifics. Means (±1 SE) are based on five replicate enclosures per treatment, with three fish per enclosure.



evidence showing that density dependence may also occur after the juvenile stage (Elliott and Hurley 1998; Jenkins et al. 1999; Bohlin et al. 2002). This phenomenon is common in lacustrine environments (Lorenzen and Enberg 2002), but its prevalence in stream fish populations may have been underestimated to date because of the bias in the literature towards salmonid species, which frequently engage in strong territorial competition as juveniles (Le Cren 1973; Elliott 1990; Grant and Kramer 1990).

Bullheads grew faster at reduced density and also underwent a dietary shift, eating fewer *Baetis* nymphs and chironomid larvae and tending to consume more *G. pulex*. Similar changes were observed when densities of invertebrate prey were elevated above ambient levels. These parallel responses to manipulation of both fish density and resource availability indicate that bullheads were food limited at high density and, in conjunction with the lack of evidence for interference competition (see below), support the hypothesis that exploitation competition for food was the primary cause of the density-dependent growth observed in experiment 1. In both experiments, bullheads grew more slowly with increasing per capita food competition despite maintaining total prey biomass consumption. Bullheads can adopt a flexible, opportunistic foraging strategy in response to fluxes of key invertebrate groups (Mann and Orr 1969; Welton et al. 1983) but prefer large, mobile species such as *G. pulex* (Smyly 1957; Welton et al. 1983). The importance of *Gammarus* was confirmed in the present study, where they consistently accounted for >60% of prey biomass consumed by bullheads in enclosures, and also in free-ranging fish in the Brandy Stream (A.J.H. Davey, unpublished data). While flexible foraging by fish can ameliorate the effects of competition (Nakano et al. 1999), in the present study, it appears that bullheads suffered reduced growth despite a dietary shift because the alternative prey (chironomid and simuliid larvae) were less profitable than *Gammarus*.

Although strong effects of stream predators on invertebrate prey densities are well documented (Wooster 1994; Dahl and Greenberg 1996; Shurin et al. 2002), this study provides the strongest evidence to date that density dependence in fish can be caused solely by exploitation competition for prey. Positive responses of fish to food addition indicate that food availability may be a limiting factor in some systems (Boss and Richardson 2002). In territorial species, interference competition can reduce the food intake of subordinate individuals (Elliott 2002) and food availability can indirectly influence rates of mortality and emigration through an effect on territory size (Keeley 2000, 2001). Jenkins et al. (1999) speculated that density-dependent growth of brown trout at low densities might be due to reduced prey consumption caused by antipredator behaviour by baetid mayfly nymphs. Other studies have found no evidence for density-dependent prey consumption (Forrester et al. 1994). Despite a lack of empirical evidence, theory suggests that exploitation competition may be more common than currently believed. In temperate environments, seasonal variation in prey abundance and water temperature may lead to periodic bouts of intraspecific competition when food abundance is low relative to the metabolic demands of the population (Persson and Johansson 1992; Boss and Richardson 2002). These resource bottlenecks can affect postrecruit as well as prerecruit life stages and could explain the strong exploitation competition observed among adult bullheads in the Brandy Stream.

In contrast with the strong influence of exploitation competition on bullhead performance, we found little evidence for interference competition: although level of isolation had some minor effects of on prey consumption, both mean growth rate and variation in growth among individual fish were unaffected. While the limited duration of the experiments meant that interference competition could not be ruled out entirely, any influence of interference was weak relative to that of exploitation competition. This was unexpected because bullheads are territorial, act aggressively towards conspecifics when active at night (Smyly 1957; Ladich 1989), and can displace smaller individuals from preferred microhabitats (Davey et al. 2005). Since level of isolation was confounded with total area available for movement, it is possible that any negative effects of interference on growth could have been obscured by a positive response of fish to reduced confinement. There was no evidence, however, that confinement ad-

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Fig. 5. Mean consumption of (*a*) *Gammarus pulex*, (*b*) chironomid larvae, (*c*) simulid larvae, and (*d*) *Baetis* nymphs by bullheads (*Cottus gobio*) in cage enclosures. Fish were exposed to two levels of food availability (ambient and elevated), both with and without barriers physically isolating conspecifics. Means (±1 SE) are based on five replicate enclosures per treatment, with three fish per enclosure.

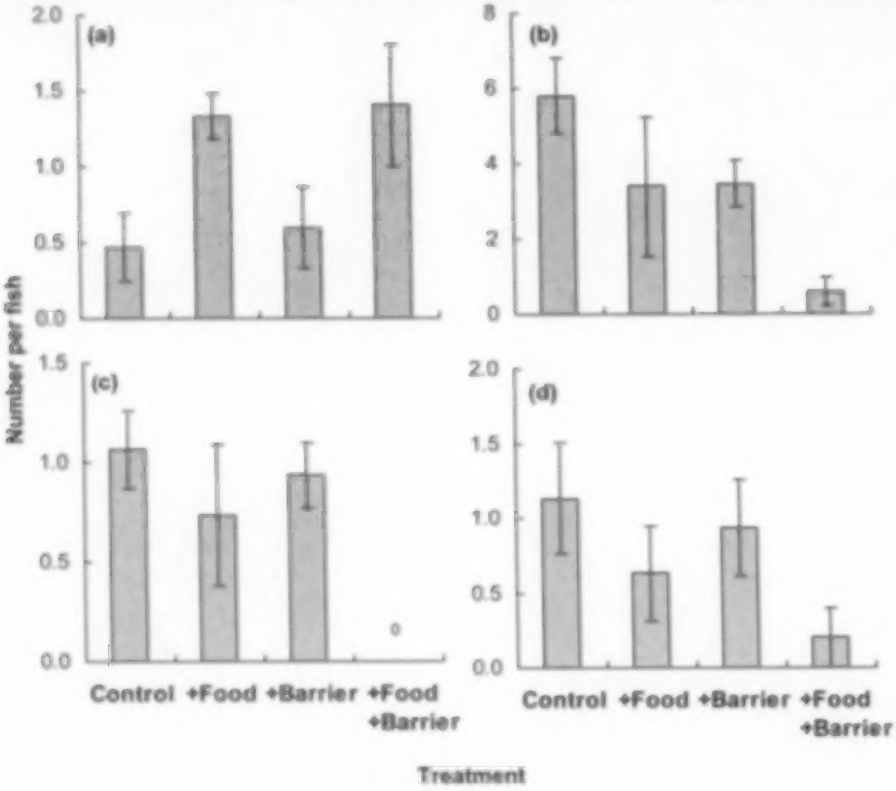
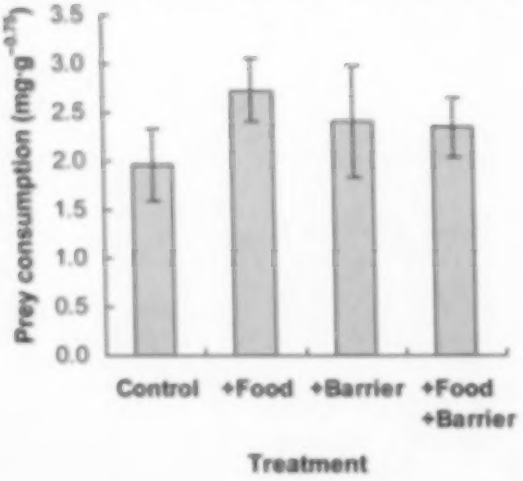


Fig. 6. Total prey biomass consumption per fish expressed as dry weight of all prey (mg) divided by fish mass to the power of 0.75 to account for the allometric relationship between body size and food consumption. Fish were exposed to two levels of food availability (ambient and elevated), both with and without barriers physically isolating conspecifics. Means (±1 SE) are based on five replicate enclosures per treatment, with three fish per enclosure.



versely affected the growth of fish. Another explanation is that the barriers may have prevented direct physical contact between fish but not other forms of interference. This too was unlikely. Extensive growth of periphyton on the mesh prevented visual contact between neighbouring fish, and chemical communication between individuals would also have been low because the barriers were aligned parallel to the water flow. Isolated fish could still communicate by sound, but bullheads produce sound only when a visual stimulus (i.e., sighting a conspecific) triggers an agonistic encounter (Ladich 1989). Consequently, we believe that the experimental manipulation provided a robust test for interference competition.

At the population level, density dependence in individual growth is likely to translate into changes in demographic parameters such as fecundity and survival. Female fecundity is positively correlated with size (Mann 1971; Fox 1978; Marconato and Bisazza 1988), and in chalk streams, where the bullhead is a fractional spawning species, larger individuals commence spawning earlier in the year and lay more batches of eggs (Fox 1978). Changes in growth rate may also affect survival: empirical relationships between body size and natural mortality (Lorenzen 1996) predict that average-sized fish from experiment 1 would have an instantaneous mortality rate of 1.94·year^{-1} after a 16-week summer growth season at high population density (7.1 fish·m^{-2}) but a

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mortality rate of only 1.57·year^{-1} if at low density (1.8 fish·m^{-2}). We stress, however, that detecting density dependence only identifies exploitation competition among adults as a potential regulating factor; further studies are required to relate individual growth rate to fitness and to compare the strength of density-dependent processes acting at different stages of the life cycle.

In summary, this study provides new insights into the mechanisms that give rise to density dependence in stream fish populations and cautions against the assumption that demographic rates of adult fish are density independent. Exploitation competition for food can lead to density-dependent growth during the adult (postrecruit) phase and may potentially regulate population size via effects on fecundity and survival.

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Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*)

Deirdre Brophy, Bret S. Danilowicz, and Pauline A. King

Abstract: Considerable debate surrounds the issue of reproductive exchange between subunits of marine fish populations. Discrete population theories predict that spawning time and location are predetermined during larval life and that spawning season fidelity and natal homing maintain population integrity. Conversely, spawning assemblages may represent interconnected subgroups within metapopulations with social transmission of spawning behaviours facilitating mixing. This study examines spawning season fidelity in three subpopulations of Atlantic herring (*Clupea harengus*) with overlapping distributions. Autumn- and winter-spawned fish were collected from spawning and feeding grounds in the Irish and Celtic seas. Hatching season was determined using otolith microstructure and was compared with season of spawning as indicated by visual gonad inspection. Spawning assemblages in the Irish Sea consisted almost exclusively of autumn-spawned fish, despite extensive mixing with winter-spawned fish during the juvenile phase. The available evidence suggests that in Celtic herring, the season and location of spawning are not learned from repeat-spawning adults, but are predetermined, possibly through larval imprinting. The seasonal components showed distinct patterns of gonad development, and estimated rates of spawning season switching were below 10%. Although this exchange rate will facilitate some gene flow, mixing of subgroups is limited. This has important implications for management of seasonal spawning populations.

Résumé : Il existe un important débat au sujet des échanges reproductifs entre les sous-unités des populations de poissons marins. Les théories démographiques discrètes prédisent que le moment et le site de la fraye sont prédéterminés durant la vie larvaire et que la fidélité à la saison de fraye et le retour au cours d'eau de naissance maintiennent l'intégrité de la population. Inversement, les rassemblements de fraye peuvent contenir des sous-groupes reliés entre eux au sein des métapopulations avec une transmission sociale des comportements de fraye qui favorise les mélanges. Notre étude examine la fidélité à la saison de fraye chez trois sous-populations du hareng atlantique (*Clupea harengus*) qui ont des répartitions qui se recoupent. Nous avons récolté des poissons nés en automne et en hiver sur les sites de fraye et d'alimentation dans la mer d'Irlande et dans la mer Celtique. La microstructure des otolithes a permis de déterminer la saison d'éclosion qui a pu être comparée à la saison de fraye déterminée d'après l'inspection visuelle des gonades. Les regroupements de fraye dans la mer d'Irlande consistent presque exclusivement de poissons issus des frayes d'automne, malgré un important mélange avec des poissons issus des frayes d'hiver durant la phase juvénile. Les données disponibles indiquent que, chez les harengs de la mer Celtique, la saison et le site de la fraye ne sont pas appris des adultes qui se reproduisent plusieurs fois, mais sont prédéterminés, peut-être par imprégnation au stade larvaire. Les composantes saisonnières incluent des patrons distincts de développement des gonades; les taux estimés de changement de saison de fraye sont inférieurs à 10 %. Bien que ce taux d'échange favorise un peu le flux génétique, le mélange des sous-groupes est limité. Ces observations ont des implications importantes pour la gestion des populations à fraye saisonnière.

[Traduit par la Rédaction]

Introduction

The mechanisms maintaining stock structure of marine fish populations are the focus of a growing body of research (Begg et al. 1999). Despite the lack of obvious physical barriers to dispersal in the marine environment and the high potential for stock mixing, genetically distinct stocks do exist in many marine fish species at varying degrees of geographical separation (Johnson et al. 1994; Ruzzante et al. 1998; McPherson et al. 2004). Even in the absence of detectable genetic variability, evidence from other methods of stock identification support the occurrence of stock structuring, with low levels of gene flow perhaps diluting the genetic variation between subpopulations (Begg 1998; Thorrold et al. 2001; Geffen et al. 2003).

The mechanisms proposed to account for structuring in marine fish populations include the timing and location of spawning in relation to oceanographic features, as well as the vertical movement of larvae (Iles and Sinclair 1982; Fortier and Leggett 1983; Rowe and Epifanio 1994), which may ensure retention close to spawning grounds, limiting dispersal and mixing of larvae from different spawning ag-

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gregations (Sinclair and Tremblay 1984; Ruzzante et al. 1998). There is also evidence that fish can return to natal spawning sites after larval or juvenile dispersal (Lockwood and Lucassen 1984; Polacheck et al. 1992; Thorrold et al. 2001). However, it is not known whether natal homing in marine fish populations is facilitated by the imprinting of spawning-ground conditions during the early life phases, or if new recruits learn spawning migrations from repeat-spawning adults through the process of social learning (Brown and Laland 2003).

The degree to which the timing of spawning restricts reproductive mixing of fish from seasonal spawning populations is not known. In many marine species, the timing of spawning shows geographical variation. The most notable examples are provided by the Atlantic herring (*Clupea harengus*). However, seasonally distinct spawning populations also occur in other pelagic, demersal, and flatfish species (Fairbairn 1981; Johnson et al. 1994; Ruzzante et al. 1998). If the timing of spawning is instrumental in the preservation of stock structure, it must be predetermined to some degree by season of hatching, with adult fish spawning in the same season in which they themselves were spawned.

There is a considerable amount of conflicting evidence with regard to the control of spawning time in marine fish populations. In their discrete population concept, Iles and Sinclair (1982) propose that timing of spawning in herring represents an adaptation to the quality of larval retention areas and is thus a predetermined trait that maintains segregation of seasonal spawning populations (Sinclair and Tremblay 1984). Although this theory is supported by the observed differences in the morphology, otolith characteristics, and life history traits of herring spawning at different times of the year (Parrish and Saville 1965; Postuma 1974), evidence from otolith morphometrics suggests that herring spawned during one season often occur in spawning aggregations in a different season (Messieh et al. 1989; McQuinn 1997*a*). Within populations of herring and other marine fish species, variation in timing of spawning has been linked to condition, size, age, and nutritional status of individual fish, as well as environmental conditions before the onset of spawning (Rajasilta 1992; Slotte 1999; Wieland et al. 2000). Such evidence highlights the phenotypic plasticity of reproductive traits and contradicts the premise that timing of spawning can maintain segregation of stocks in the absence of other barriers to gene flow.

Metapopulation theory (Levins 1968) has been applied to descriptions of stock structure in marine fish (McQuinn 1997*b*; Smedbol and Wroblewski 2002; Kritzer and Sale 2004). Within a metapopulation, subpopulations are linked by variable amounts of gene flow, while a degree of local population structuring is still maintained. McQuinn (1997*b*) has used the metapopulation concept to reconcile the conflicting evidence relating to stock structure in Atlantic herring. According to McQuinn's adopted-migrant model, spatial and temporal spawning behaviours are learned by recruiting year classes from the adults with which they associate during the prerecruitment life phases and are not predetermined by the season or location of hatching. In sympatric seasonal spawning populations, juveniles hatched in one season often associate with adults from another seasonal spawning group, and the potential exists for considerable genetic exchange.

This study examines the degree of spawning season fidelity displayed by three subpopulations of Atlantic herring in the Celtic and Irish seas that show overlapping distributions throughout the life cycle. Two herring spawning components occur in the Celtic Sea, with spawning of each group occurring within the same geographical area (Anonymous 1994). The peak period of spawning for the autumn-spawning group lasts from September–October to November. In the winter-spawning group, spawning occurs from late December to February (Molloy 1980; Anonymous 1994). In the Irish Sea, most herring spawning takes place over a 3–4 week period from late September onwards at spawning grounds off the coast of the Isle of Man (Dickey-Collas et al. 2001). During the first year of life, some herring from the Celtic Sea are transported into the Irish Sea (see Fig. 1), where autumn- and winter-spawned herring from the Celtic Sea and autumn-spawned herring from the Irish Sea occur together at nursery grounds (Brophy and Danilowicz 2002). In the current study, otolith microstructure patterns, which can be used to distinguish between autumn- and winter-spawned herring (Brophy and Danilowicz 2002), are used to establish if this extensive overlap at the prerecruitment stage results in exchange between the adult spawning populations through social learning, as predicted by the adopted-migrant hypothesis, or if larval imprinting ensures natal homing. The hypothesis that season of first reproduction is not predetermined by season of hatching is evaluated. Finally, the degree to which the timing of spawning may maintain stock structure in marine fish populations is assessed.

Methods

Sample collection

Adult herring were collected from spawning grounds in the Celtic Sea during the autumn spawning season from September to November in 1999, 2001, and 2003 and during the winter spawning season from December to February in 1999, 2000, 2001, and 2003. In August 2003, aggregations of herring on feeding grounds were sampled in the Celtic Sea; in the Irish Sea, herring were collected from the spawning grounds in 1999, 2003, and 2004 (sampling locations are shown in Fig. 2). Samples were obtained from herring acoustic surveys on board the R/V *Celtic Voyager*, the F/V *Regina Ponti*, and the R/V *Lough Foyle* and from the commercial fishery.

Fish length and weight were determined and otoliths were removed. Maturity stages were assessed by visual inspection of the gonads using an eight-point maturity scale (Anonymous 1962; Landry and McQuinn 1988).

Determination of hatching season using otolith microstructure

After removal, sagittal otoliths were stored overnight in water-filled vials to improve the contrast between the opaque region of summer growth and the translucent winter ring. Otoliths were then placed on a black background and examined through an Olympus™ SX9 binocular microscope (Olympus, Hamburg, Germany) using 40× magnification. Fish ages were determined by counting growth zones. A

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Fig. 1. Principal herring (*Clupea harengus*) spawning locations in the Celtic and Irish seas, with arrows indicating dispersal of Celtic Sea herring to nursery grounds in the Irish Sea. Solid and shaded ellipses denote spawning areas for autumn and winter spawning fish, respectively.

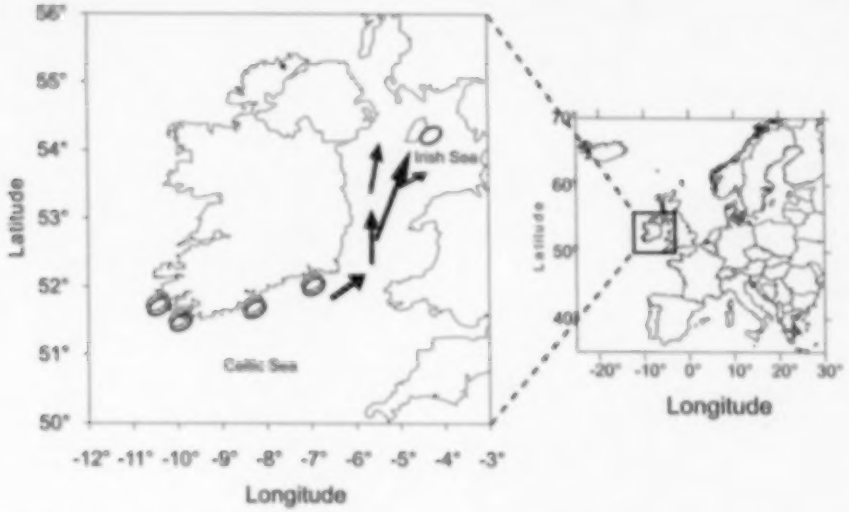
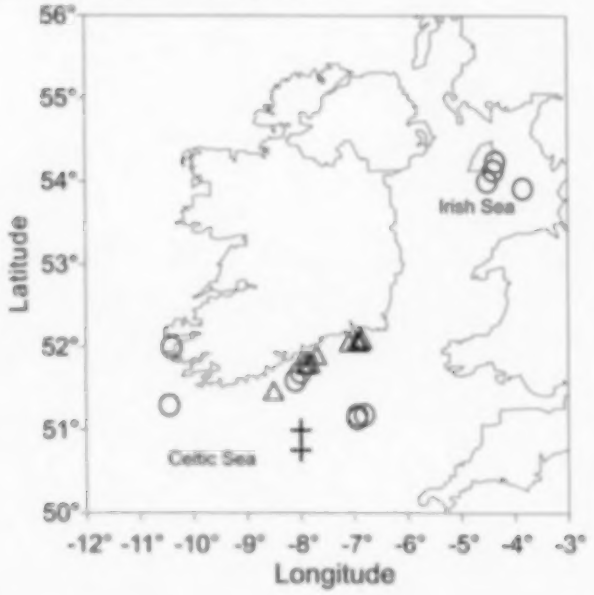


Fig. 2. Locations of herring (*Clupea harengus*) samples collected during the autumn (○) and winter (△) spawning seasons and from feeding grounds in August (+).



complete growth zone was identified as one opaque summer growth region and one translucent winter growth region. After age determination, otoliths were dried in air, mounted in epoxy resin using small circular moulds (5 mm diameter), and polished on the antisulcal side using 2000 and 4000 grit silicon carbide paper until a flat otolith surface was obtained. The mounted otoliths, still contained within the blocks of resin, were then remounted using larger moulds (10 mm diameter) and polished on the sulcal side until the primordium was exposed. Polishing on each side removed excess material from the otolith section, which enhanced visibility of the core region. Mounted otoliths were examined using a light microscope at a magnification of 1000×. Otolith microstructure measurements were made using a digital CCD camera and image analysis software (Optimas 6.1, MediaCybernetics Inc., Silver Spring, Maryland; Olympus DP-Soft, Olympus, Hamburg, Germany). Larval increment widths were measured from the first visible increment out to 200 µm along the longest axis. Mean otolith increment width measurements in the region 60–70 increments from the core were used to identify the season in which each adult fish was spawned, as the growth patterns of the autumn- and winter-spawned group are most distinct in this otolith region. Fish with a mean otolith increment width of ≤2.2 µm at increments 60–70 were classified as autumn-spawned, whereas fish with mean increment widths of ≥2.3 µm were identified as winter-spawned. These limits were determined from the bimodal distribution of mean increment widths observed in winter- and autumn-spawned 0-group herring from the 1998–1999 and the 1999–2000 year classes collected from nursery grounds in the Irish and Celtic seas (Brophy and Danilowicz 2002).

The adult samples used in the present study were collected over five spawning seasons and incorporated several year classes. Variation in otolith growth between year classes, which could potentially reduce the accuracy of spawning season determination, was investigated for the autumn- and winter-spawned fish in both seas separately using one-way analysis of variance (ANOVA), with year class as the single fixed factor and mean increment width at increments 60–70 as the dependent variable. Year classes for which low numbers of fish were available (<5) were omitted from the analysis.

Temporal distribution and gonad development rates of autumn- and winter-spawned herring

The numbers of fish of both otolith types at each developmental stage and in each sampling period were summarised

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in a series of contingency tables. The hypothesis that fish that had hatched in autumn and winter formed a single stock unit with a homogenous temporal distribution and that the two otolith types were equally likely to occur in samples collected in summer, autumn, and winter was tested using a χ^2 test. Percentage values were used to remove variation resulting from differences in sampling effort between the seasons. The χ^2 analysis was also used to test the null hypothesis of no association between gonad development and otolith type (season of hatching) within each sampling period (summer, autumn, and winter). When necessary, gonad stages were pooled into fewer divisions to avoid low cell frequencies in the contingency table.

Estimation of spawning season fidelity

Spawning season fidelity was assessed by comparing the season of hatching, as determined from the microstructure measurements, with season of spawning, as indicated by stage of gonad development. In the Celtic Sea, fish that spawn in autumn and winter may occur at the same stage of gonad development at certain times of the year. For example, a fish collected from the spawning grounds in November at stage 5 could potentially spawn in the autumn or delay spawning until winter. Only fish that could be unambiguously assigned to a spawning group were included in estimates of spawning season fidelity. Fish that were collected in spawning condition (stage 6) were assigned to the spawning season in which they were captured. Fish collected in spent condition in autumn (stages 7 and 8) and in prespawning condition (stage 5) in winter were assigned to the autumn and winter spawning groups, respectively. For herring in the prespawning stages (stages 4 and 5) in autumn and in spent condition (stages 7 and 8) in winter, the timing of spawning could not be conclusively determined and so these fish were not included in estimates of spawning season fidelity.

Results

Determination of hatching season using otolith microstructure

Otolith increment widths at increments 60–70 in adult herring otoliths showed a clear bimodal distribution, with values falling within the range reported by Brophy and Danilowicz (2002) for autumn- and winter-spawned juvenile herring (Fig. 3). Mean increment widths for adult fish identified as autumn- and winter-spawned were 1.5 µm and 3.6 µm, respectively. These values are comparable with the means observed in juvenile fish (1.4 µm and 1.6 µm for autumn-spawned fish collected in 1999 and 2000, respectively; 3.3 µm and 3.5 µm for winter-spawned fish collected in 1999 and 2000, respectively). For the Celtic Sea fish, both the autumn- and the winter-spawned group showed no significant variation in otolith increment widths at increments 60–70 among year classes (ANOVA, $p = 0.65$ and 0.115, respectively). Similarly, for the autumn-spawned fish from the Irish Sea, no significant differences in the increment width measurements were observed between year classes ($p = 0.114$). In a small number of the otoliths examined, the mean increment width in the region of interest was 2.3 µm and the fish were identified as winter-spawned. This is very close to the previously recorded upper limit of the autumn-spawned fish of 2.2 µm and may represent a region of overlap between the two groups. However, this affected a total of two fish only, which were collected in autumn at stage-5 maturity stage and so their inclusion in the analysis does not affect the conclusions on spawning season fidelity.

Composition of Irish Sea spawning aggregations

Samples of mature adults from the Irish Sea spawning grounds consisted almost exclusively of autumn-spawned fish (98%). In other words, the majority of herring sampled from the spawning aggregations around the Isle of Man were spawning in the same season in which they themselves were spawned (Fig. 3; Table 1).

Temporal distribution of autumn- and winter-spawned herring in the Celtic Sea

In the Celtic Sea, the distribution of autumn- and winter-spawned fish overlapped in all sampling periods, with the winter spawning component dominating throughout the year. For fish collected during the autumn spawning season, 33% were classified as autumn-spawned, and 67% as winter-spawned according to their mean increment widths at increments 60–70. For fish collected in the winter, 95% were identified as winter-spawned, and 5% as autumn-spawned. For the samples collected on the feeding grounds in August, 80% were identified as winter-spawned, and 20% as autumn-spawned (Fig. 3; Table 2). The relative proportions of the two otolith types varied significantly with sampling time (Pearson's $\chi^2 = 25.1$, $p < 0.001$). The standardised deviations of the observed and expected values showed that the proportion of autumn-spawned fish was lower than the expected value among samples collected in winter and higher than the expected value in the autumn samples. The reverse trend was true for the winter-spawned fish. In the summer sample, there was little difference between the observed and expected values with standardised deviations of less than 1 (Table 2). These results confirmed that the autumn- and winter-spawned fish do not form a homogenous group and display distinct temporal distributions.

Gonad development patterns in autumn- and winter-spawned herring

The χ^2 analysis of separate contingency tables for each sampling period showed that the autumn- and winter-spawned fish displayed distinct patterns of gonad development. For the summer samples, the null hypothesis of no association between otolith type and gonad stage was rejected (Pearson's $\chi^2 = 21.0$, $p < 0.001$). The standardised deviant values showed that there were less autumn-spawned fish at stage 3 and more at stage 4 and 5 than expected (Table 3*a*). The reverse pattern was observed for the winter-spawned fish. Cochran's test confirmed that the proportion of autumn-spawned fish increased linearly with increasing stages of development, whereas the proportions of winter-spawned fish decreased (18.8, $p < 0.001$). The χ^2 test of association also yielded a significant result for fish collected in autumn (Pearson's $\chi^2 = 37.9$, $p < 0.001$). Again, the observed frequency of autumn-spawned fish was lower than expected at stages 4 and 5 and higher than expected at stages 6–7, with

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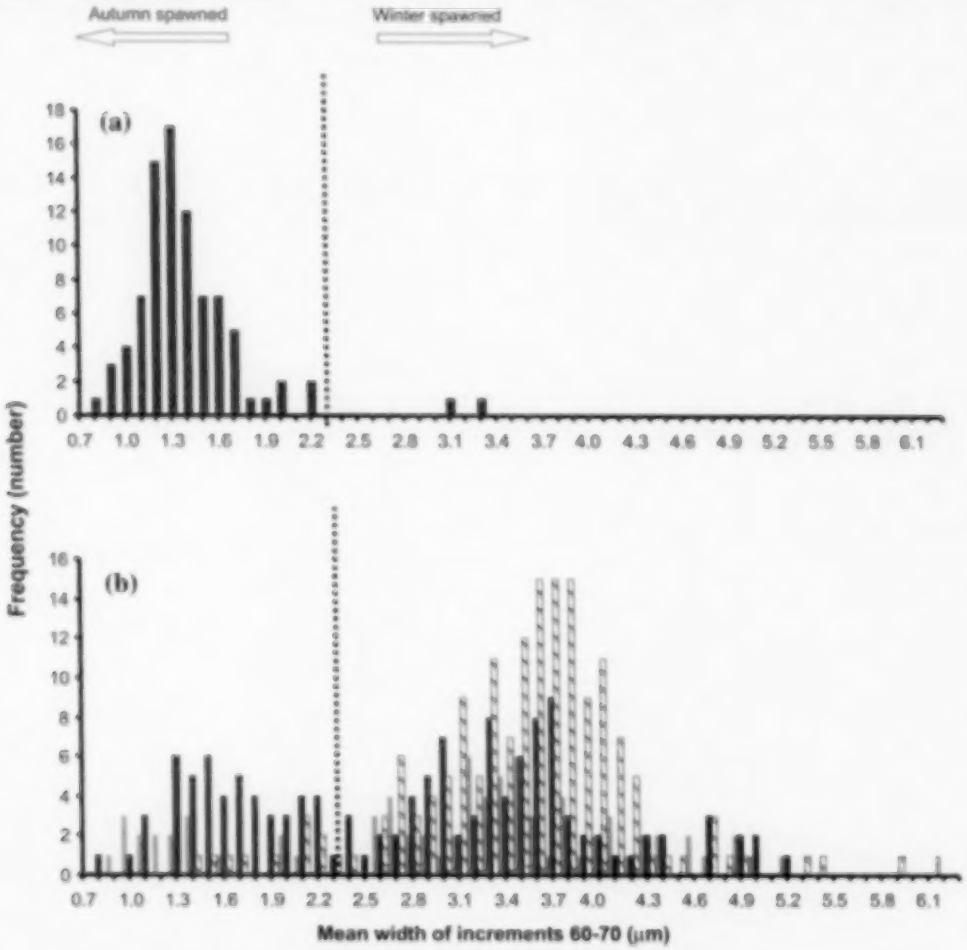
Fig. 3. Distribution of mean larval increment widths at increments 60–70 in adult herring (*Clupea harengus*) collected from (*a*) the Irish Sea and (*b*) the Celtic Sea. Solid bars represent fish collected in autumn, shaded bars represent fish collected in summer, and hatched bars represent fish collected in winter.


Autumn spawned
Winter spawned
(a)
(b)
Frequency (number)
Mean width of increments 60-70 (μm)
0.7 1.0 1.3 1.6 1.9 2.2 2.5 2.8 3.1 3.4 3.7 4.0 4.3 4.6 4.9 5.2 5.5 5.8 6.1

the winter-spawned fish showing the opposite trend (Table 3*b*). The proportion of autumn-spawned fish increased linearly with increasing stages of development, whereas the proportions of winter-spawned fish decreased (Cochran's linear trend statistic = 34.3, $p < 0.001$). When all prespawning fish were combined in a single category, the spawning and spent fish were 12 times more likely to be autumn-spawned than winter-spawned (odds ratio = 12.5, $p < 0.05$, 95% confidence interval (CI) 4.7 to 32.9).

Similarly, for the fish collected in winter, stage of gonad development was not independent of otolith type (Yate's corrected χ^2 for small sample sizes = 10.8, $p = 0.001$). The frequency of autumn-spawned fish was lower than expected at stages 5–6 and higher than expected at stages 7–8 and vice versa for the winter-spawned fish (Table 3*c*). The prespawning and spawning fish were 10 times more likely to be winter-spawned than autumn-spawned (odds ratio = 10.1, $p < 0.05$, 95% CI 2.3 to 44.1). The summary statistics from the contingency table analyses are shown in Table 4.

Estimation of spawning season switching rates

The incidence of spawning season switching in the Celtic Sea was difficult to assess directly, as the timing of spawning could not be ascertained for all fish. Of the herring that were collected from spawning grounds in winter in prespawning or spawning condition (stages 5 and 6), 2% had otoliths of the autumn-spawned type and were therefore spawning outside of their season of hatching. During the autumn spawning season, the number of fish that were spawning or spent when sampled, and for which autumn spawning could be confirmed, was low (24 fish). The larval microstructure analysis showed that 23% of these fish had hatched in winter and subsequently switched spawning season. To estimate the rate of spawning season switching, the relative abundance of the autumn- and winter-spawned components in the Celtic Sea must be known. The proportions of each group varies throughout the year as fish move towards and away from the spawning grounds according to their spawning condition. It is likely that the aggregations of fish at the

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Table 1. Numbers of autumn- and winter-spawned fish (as determined by otolith microstructure) at each stage of gonad maturity for each sampling period and location, pooled across years.

		Otolith type	
Collection	Gonad stage	Autumn spawned	Winter spawned
Irish Sea, autumn	3	2	
	4	5	
	5	82	2*
	6	2	
	7/8	7	
Celtic Sea, August	3	2	38
	4	10	30
	5	6	2
Celtic Sea, autumn	4	1	21
	5	24	71
	6	21	5*
	7/8	3	2*
Celtic Sea, winter	5		13
	6	3*	123
	7/8	6	27

Note: The shaded areas highlight the gonad stages at which season of spawning could be ascertained. Asterisks indicate fish spawning outside of their season of hatching.

Table 2. Contingency table showing the percentages and observed and expected frequencies of autumn- and winter-spawned fish occurring in samples collected from the Celtic Sea at different times of the year.

	Otolith type	
Sampling period	Autumn spawned	Winter spawned
Summer		
Observed frequency	18	70
Observed percentage	20.5	79.5
Expected percentage	19.7	80.3
Standardised deviate[a]	0.18	−0.09
Autumn		
Observed frequency	49	98
Observed percentage	33.3	66.6
Expected percentage	19.7	80.3
Standardised deviate	3.1	−1.5
Winter		
Observed frequency	9	163
Observed percentage	5.2	95.8
Expected percentage	19.7	80.3
Standardised deviate	−3.3	1.6

Note: The standardised deviate measurements show how observed frequencies differ from the frequencies expected if there were no association between sampling time and otolith type.

[a](Observed − expected)/$\sqrt{\text{expected}}$).

feeding grounds, before the start of spawning activity and spawning-ground migrations give the most accurate reflection of the relative proportions of the two components. In this study, 20% of samples collected from the feeding grounds were autumn-spawned fish (Table 2). The relative proportions remained fairly constant across individual hauls,

Table 3. Contingency tables showing the percentage and observed and expected frequencies of fish at various stages of gonad development among autumn- and winter-spawned fish collected during (*a*) summer, (*b*) autumn, and (*c*) winter in the Celtic Sea.

(*a*) Fish collected during summer.

	Gonad development stage		
Otolith type	3	4	5
Autumn spawned			
Percentage	11.1	55.6	33.3
Observed frequency	2	10	6
Expected frequency	8.2	8.2	1.6
Standardised deviate	−2.2	0.64	3.4
Winter spawned			
Percentage	54.3	42.8	2.9
Observed frequency	38	30	2
Expected frequency	31.8	31.8	6.4
Standardised deviate	1.1	−0.32	−1.73

(*b*) Fish collected during autumn.

	Gonad development stage		
Otolith type	4	5	6–7
Autumn spawned			
Percentage	2.0	49.0	49.0
Observed frequency	1	24	24
Expected frequency	7.3	31.3	10.3
Standardised deviate	−2.3	−1.3	4.3
Winter spawned			
Percentage	21.4	71.4	7.1
Observed frequency	21	70	7
Expected frequency	14.7	62.7	20.7
Standardised deviate	1.6	0.9	−3.0

(*c*) Fish collected during winter.

	Gonad development stage	
Otolith type	5–6	7–8
Autumn spawned		
Percentage	33.3	66.7
Observed frequency	3	6
Expected frequency	7.3	1.7
Standardised deviate	−1.6	3.2
Winter spawned		
Percentage	83.4	16.6
Observed frequency	136	27
Expected frequency	131.7	31.3
Standardised deviate	0.37	−0.76

Note: The standard deviate measurements show how observed frequencies differ from the frequencies expected if were there no association between otolith type and gonad development.

with the percentage of autumn-spawned fish ranging from 19.2% to 21.6%. The percentage of fish that spawned outside of their season of hatching, assuming that the autumn-spawned fish represent 20% of the numbers of adult herring in the Celtic Sea, was estimated by raising the numbers of autumn-spawned fish by a factor of five to give equal weighting to each component. Using the weighted data, the level of spawning season switching was estimated as 5.5% and 9.9% for winter- and autumn-spawned fish, respectively

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Table 4. Summary statistics from the contingency table analyses of frequencies of autumn-spawned (AS) and winter-spawned (WS) fish within categories of gonad development and sampling time.

	χ^2	Cochran's statistic	Odds ratio	95% CI
Sampling time × otolith type (Table 2; 3×2)	25.1 ($p < 0.001$)			
Otolith type × gonad stage				
Summer (Table 3*a*; 2×3)	21.0 ($p < 0.001$)	18.8 ($p < 0.001$)		
Autumn (Table 3*b*; 2×3)	37.9 ($p < 0.001$)	34.3 ($p < 0.001$)	12.5*	4.7 to 32.9
Winter (Table 3*c*; 2×2)	10.4 ($p = 0.001$)		10.1†	2.3 to 44.1

Note: CI, confidence interval.
*AS vs. WS in spawning and spent fish.
†WS vs. AS in ripe and spawning fish.

(Table 5). This was the best approximation that could be obtained from the available data. Although it cannot be taken as an exact measure, it indicates that the average rate of spawning season switching is similar for each component and that the rate of exchange between the two groups, although low, is enough to facilitate gene flow between the two groups (assuming that the offspring of the spawning season switchers survive to reproduce).

Discussion

The bimodal distribution of otolith increment widths, which distinguishes autumn- and winter-spawned fish, showed little temporal variability. There was no significant variation in otolith increment widths among year classes of autumn- and winter-spawned adult herring in both seas. In addition, the range of increment widths reported in the present study for adult herring is similar to that reported for juvenile herring from the Irish and Celtic seas (Brophy and Danilowicz 2002). Otolith increment width measurements appear to allow accurate classification of autumn- and winter-spawned fish for the year classes included in the present study.

Herring from the two Celtic Sea spawning components occur together on the spawning grounds during autumn and winter and in summer feeding aggregations but display different rates of gonad development. Although fish were observed to spawn outside of their season of hatching, the rate of spawning season switching was low. In the Celtic Sea, the timing of spawning is largely predetermined by season of hatching and is thus instrumental in the preservation of stock structure. Although the seasonal components do not show random mixing, there is sufficient exchange between seasons through occasional spawning season switching to keep these seasonal stocks genetically mixed. Also, these findings do not refute the possible influence of the environment on spawning time in Atlantic herring. Herring may possibly respond to environmental conditions before and during gonad development and adjust their maturation patterns in accordance with the expected environment at the time of spawning. In this way they could ensure that their eggs and larvae are exposed to conditions similar to those of the environment in which they themselves hatched and survived and are presumably best adapted. Large and sudden changes in the prespawning environment may lead to spawning season switching, as suggested by Aneer (1985). However, under average environmental conditions, adult herring will tend to spawn in the same season in which they themselves were spawned, thus preserving the integrity of sympatric populations.

Although the occurrence of winter-spawned fish in catches of spawning and spent fish in autumn remained low, most ripe (stage 5) herring collected on the spawning grounds in autumn had hatched in winter. Previous studies have shown that winter and spring spawning herring reach late stages of gonad development before the onset of winter and remain at this stage for prolonged periods of up to 3 months (Iles 1964; McQuinn 1989). It is likely that ripe winter-spawned fish collected at Celtic Sea spawning grounds in autumn delay spawning until winter. This justifies their exclusion from the assessment of spawning season fidelity.

The results reported here are at odds with McQuinn's (1997*a*) study of sympatric herring populations in the Northwest Atlantic, which reports considerably higher levels of crossover between spring and autumn spawning herring. The discrepancy between McQuinn's results and the current study may reflect a difference between the stocks under investigation or may arise as a result of methodological differences. In his assessment of spawning season fidelity, McQuinn used otolith characteristics of all mature fish to infer spawning season switching, including fish from periods of overlapping development (e.g., stage-4 fish in September). The maturity stages of fish identified as "spawning season switchers" are not described, so it is not possible to assess if their inclusion could greatly influence the interpretation of the results. McQuinn's study employs visual inspection of the opacity and size of the otolith nucleus to identify the hatching season of adult fish. Although the separation of spawning types using this method was executed with high between-reader precision, inaccuracies are likely due to variation in otolith characteristics between year classes, overlap in nucleus size between groups, and the occurrence of intermediate otolith types (Postuma 1974; Cleary et al. 1982). The method used in the current study to determine season of hatching has been validated using incremental counts of juvenile otoliths and shows low levels of variation between year classes and little overlap between groups. Higher estimates of spawning season fidelity in the Northwest Atlantic herring populations might have been obtained if the otolith microstructure method was used to identify hatching season and overlapping developmental stages were omitted.

Fish collected from spawning aggregations in the Irish Sea spanned several year classes. Just over one-third of the

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Table 5. Estimated rates of spawning season switching, assuming that the winter spawning component outnumbers the autumn spawning component in the Celtic Sea by a factor of 5.

	Otolith type		
	Autumn spawned		Winter spawned
	n	Raised *n* (5*n*)	*n*
Fish spawning in autumn	24	120	?
Fish spawning in winter	3	15	136
Spawning season switching (%)		5.5	9.9
Spawning season fidelity (%)		94.5	90.1

sampled fish (42 fish) originated from the 1999 and 2000 year classes, which were observed to mix with the Celtic Sea winter spawning stock as juveniles (Brophy and Danilowicz 2002). The occurrence of juvenile Celtic Sea herring at Irish Sea nursery grounds has long been acknowledged (Bowers 1964; Molloy and Corten 1975; Molloy 1980). The dispersal pattern is consistent with oceanographic evidence of a northward flow through the St. George's Channel into the Irish Sea (Bowden 1950) and is supported by previous larval drift studies (Özcan 1974). It is likely that this is a regular annual occurrence and that all year classes examined in this study had mixed with the Celtic Sea stock during the first year of life.

The results of this study provide no support for the social transmission of spawning behaviours from adults to the recruiting year classes and contest the adopted-migrant concept. The dispersal of winter-spawned Celtic Sea herring into the Irish Sea is extensive, and they have been shown to outnumber the autumn-spawned juveniles at stations to the east and west of the Isle of Man (Brophy and Danilowicz 2002). Before recruitment, these winter-spawned herring from the Celtic Sea are likely to encounter adults from the autumn spawning Irish Sea stock rather than winter spawning adults from their parent stock. Nonetheless, the winter-spawned herring, which dominated the nursery areas as juveniles, are virtually absent from adult aggregations in the Irish Sea and evidently do not adopt the spawning behaviour of the adult stock. Similarly, the autumn and winter spawning components in the Celtic Sea show extensive overlap in their range throughout the life cycle. Spawning of each group occurs within the same geographical area (Anonymous 1994), and autumn- and winter-spawned juveniles occupy the same nursery areas (Brophy and Danilowicz 2002). Therefore, the temporal separation of spawning in the two groups does not occur simply as a result of the juveniles adopting the maturation patterns of the adults in the vicinity.

Historically, there has been no winter herring fishery in the Irish Sea and only low and infrequent levels of winter spawning have been observed (Dickey-Collas et al. 2001). Therefore the large numbers of winter-spawned herring from the Celtic Sea, which move into the Irish Sea during the first year of life, leave the Irish Sea as adults to spawn elsewhere. This spawning migration is evidently not learned from repeat spawners. So do the Celtic Sea winter-spawned herring, which may disperse into the Irish Sea as early as within the first month after hatching (Brophy and Danilowicz 2002), subsequently home to their parent stock in the Celtic Sea? Juveniles tagged in the Irish Sea have been recaptured as adults in spawning aggregations in the Celtic Sea (Molloy et al. 1993), indicating that the migrants do recruit to the Celtic Sea spawning stock. The natal homing hypothesis is also supported by the occurrence in the Celtic Sea winter fishery of adults with small back-calculated lengths at age 1 (from otolith annular measurements), which is characteristic of juvenile growth at Irish Sea rather than Celtic Sea nursery grounds (Brophy and Danilowicz 2003). The available evidence suggests that in the Celtic Sea winter-spawned population, the season and also the location of spawning are not learned from repeat-spawning adults but may be predetermined during the larval phase, possibly through larval imprinting.

The term larval imprinting refers to a specialised type of irreversible learning that occurs during a sensitive period of development. Although the phenomenon has been extensively studied in salmon (Dittman and Quinn 1996), evidence for its occurrence in marine fish populations, particularly in the pelagic environment, is lacking. Imprinting of spawning-ground conditions and subsequent natal homing of spawning adults requires that fish larvae possess sufficient sensory abilities to detect the environmental characteristics of the spawning ground and are capable of storing this information through spatial learning. Morphological and experimental studies show that sensory systems of larval and premetamorphic fish are adequately developed to respond to multiple olfactory, visual, and physical cues at least over small spatial scales (Kingsford et al. 2002). There is evidence that adult fish are capable of spatial learning (Odling-Smee and Braithwaite 2003) and can use learned sensory information to re-orientate themselves after displacement (Mitamura et al. 2005). Larval and presettlement reef fish may also use sensory cues to ensure retention close to natal reefs (Atema et al. 2002; Mitamura et al. 2005). However, the critical question of whether or not larval fish can store this sensory information to aid in the later location of natal spawning grounds by settling juveniles or spawning adults after a dispersive larval phase remains unanswered.

In the absence of strong support or a verified mechanism for larval imprinting, discussions of migration patterns in marine fish populations are increasingly focusing on the transmission of spawning behaviours from adults to recruits (Rose 1993; McQuinn 1997*b*; Corten 2001). The results of this study and evidence from other species (Lockwood and Lucassen 1984; Polacheck et al. 1992) show that naïve juveniles do not need to encounter repeat spawners to locate their parental spawning areas. Although the social transmission of migration routes may occur in some populations, the importance of larval imprinting in maintaining stock structure should not be overlooked. Further investigation into the mechanisms facilitating natal homing in the pelagic marine environment is warranted.

The results of this study are of relevance to the assessment and management of the associated fisheries. The Celtic Sea herring that disperse and outnumber the resident popula-

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tion at Irish Sea nursery grounds do not generally recruit to the Irish Sea fishery. Therefore juvenile abundance estimates do not provide a reliable recruitment index for this stock unless the identification of spawning season using otolith microstructure is incorporated into annual abundance surveys. The absence of recruitment of Celtic Sea herring to the Irish Sea stock justifies the separate management of the adult fisheries. In the Celtic Sea, the herring exploits a winter spawning component and a less abundant autumn spawning component. Reproductive exchange between the subgroups is limited, and therefore fishing mortality in one component is not replenished by recruitment from the other. If the seasonal groups show variation with respect to productivity and population dynamics, this could produce bias in the assessment of the fishery as a single stock, resulting in underestimation of fishing effort (Daan 1991). Further research is needed into interstock differences in life history traits, which may result in differential exploitation of the stock components.

The results of this study show that the season of spawning is largely predetermined by season of hatching in herring populations of the Celtic and Irish seas and that reproductive exchange between temporal spawning groups is limited. The timing of spawning can maintain segregation of marine fish populations in the absence of other barriers to gene flow. This has important implications for the management of temporal spawning populations. Recruitment to adult herring stocks does not rely on social transmission of spawning behaviours, and herring may home to their parental stocks by imprinting during the larval phase.

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Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroselachus crepidater*

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Abstract: Bands on the external surface of the second dorsal-fin spine proved to be a novel method of estimating the age and growth of *Centroselachus crepidater*. Bands that followed the shape of the spine base were enhanced with an alizarin red derivative. Internal bands in spine cross sections were also examined. The number of both external and internal bands increased with animal size, although most spines had more external than internal bands. External bands were more reliable and were assumed to be annuli. The rate of band formation differed after five bands had been formed, and internal bands ceased forming after 30 years. Females to 54 years old and males to 34 years old were examined. Maturity occurred over a wide age range, with estimates of 20 years for females and 9 years for males. The youngest pregnant female was 27 years old. The Francis reparameterized von Bertalanffy growth model found similar growth for males and females, and the von Bertalanffy equations were $L_t = 96.12(1 - e^{(-0.072(t+6.13))})$ for females and $L_t = 73.22(1 - e^{(-0.141(t+2.99))})$ for males.

Résumé : L'étude des bandes sur la surface externe de la seconde épine dorsale s'est avérée être une nouvelle méthode d'estimation de l'âge et de la croissance chez *Centroselachus crepidater*. Nous avons accentué le contraste des bandes qui suivent la forme de la base de l'épine à l'aide d'un dérivé du rouge d'alizarine. Nous avons aussi examiné les bandes internes sur des coupes transversales d'épines. Le nombre de bandes, tant externes qu'internes, augmente en fonction de la taille de l'animal, bien que la plupart des épines portent plus de bandes externes qu'internes. Les bandes externes sont plus fiables et nous considérons qu'il s'agit d'annulus. Le taux de formation des bandes est différent après la formation des cinq premières bandes et la formation de bandes internes cesse au bout de 30 ans. Nous avons examiné des femelles d'âge maximal de 57 ans et des mâles de 34 ans. La maturité est atteinte sur une gamme étendue d'âges et nous estimons l'âge de la maturité à 20 ans chez les femelles et de 9 ans chez les mâles. La femelle gravide la plus jeune avait 27 ans. Le modèle de croissance de von Bertalanffy avec les paramètres déterminés par la méthode de Francis indique une croissance semblable chez les mêles et les femelles; les équations de von Bertalanffy sont L_t des femelles = $96{,}12(1 - e^{(-0{,}072(t+6{,}13))})$ et L_t des mâles = $73{,}22(1 - e^{(-0{,}141(t+2{,}99))})$.

[Traduit par la Rédaction]

Introduction

Deepwater dogfishes are a major bycatch component of many of the world's demersal fisheries, and several species are directly targeted for the shark fillet and liver oil markets. In Australia, deepwater dogfishes are primarily caught as byproduct to demersal trawl fisheries, and the estimated annual value of deepwater dogfishes exceeds AU$1.5 million (Daley et al. 2002). In 2005, eight species of deepwater dogfishes, including the golden dogfish, *Centroselachus crepidater* (Bocage and Capello 1864), became managed under a "basket" quota system, with a total allowable catch set at 200 tonnes (P. Shoulder, Australian Fisheries Management Authority, P.O. Box 7051, Canberra Business Centre, ACT, Australia 2610, personal communication).

Centroselachus crepidater is uniformly dark brown to black, with a slender body, long snout, and small dorsal-fin spines. It occurs on the continental and insular slopes in depths of 270–1300 m in the eastern Atlantic (Iceland to southern Africa), the Indian Ocean (Aldabra Islands and India), the eastern Pacific (northern Chile), and western Pacific and eastern Indian oceans (New Zealand and southern Australia) (Last and Stevens 1994).

Age information forms the basis for the calculations of growth rate, mortality rate, and productivity, making it one of the most influential biological variables for estimating

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population status and assessing the risk associated with exploitation (Ricker 1975; Musick et al. 2000; Campana 2001). Band counts from vertebrae are the most commonly used method for ageing elasmobranchs (Cailliet and Goldman 2004), although most dogfish vertebrae are poorly calcified with no visible banding (Jones and Geen 1977).

Kaganovskaia (1933) first used the second dorsal-fin spine to age the spiny dogfish (*Squalus acanthias*), and the structure and function of dorsal-fin spines has since been documented (Maisey 1979; McFarlane and Beamish 1987). *Squalus* species often have spines with a banding pattern on an enamel cap, and these bands are more commonly used to age dogfishes (Holden and Meadows 1962; Nammack et al. 1985; McFarlane and Beamish 1987). However, most deepwater dogfish spines do not possess an enamel cap, and Tanaka (1990) reported an alternative ageing technique using an internal banding pattern in the spine cross sections (hereafter called "internal bands"). Over the past decade, these internal bands have been used to age several deepwater dogfishes (e.g., Tanaka 1990; Guallart Furio 1998; Clarke et al. 2002*b*). However, most studies report the usefulness of spines as a tool for ageing rather than estimating growth, and the validation of deepwater dogfish age estimates has never been attempted.

Holden and Meadows (1962) were the first to note the growth bands on the stem of the *S. acanthias* spine. In this species, each band followed the shape of the spine base and could only be counted after removing the enamel cap. The number of these external bands matched the number of enamel bands. However, because of the relative ease in counting bands on the enamel cap, the use of external base bands (hereafter called "external bands") has not been investigated.

Holden and Meadows (1962) suggested that spine growth resembled the stacking of paper cups. However, the growth of the *C. crepidater* spine is assumed to be similar to that of *S. acanthias* as described by Beamish and McFarlane (1985). In this case, upward growth is caused by deposition of dentine at the spine base, and outward spine growth is caused by the production of cartilage and dentine at the spine centre. Therefore the formation of external bands (and enamel bands) is independent of inner dentine band formation.

This study reports an alternative method of ageing deepwater dogfishes and constitutes the first investigation into the age and growth of any deepwater shark in the southern hemisphere. More traditional ageing methods using internal bands were also tried, and the results were compared with those of our technique.

Materials and methods

Sample collection

Between November 2000 and July 2002, *C. crepidater* were opportunistically collected from the bycatch of commercial fisheries operating in southeastern Australia (Fig. 1). Fishers were primarily targeting orange roughy (*Hoplostethus atlanticus*) and most *C. crepidater* were collected from depths of 650–1000 m.

Each dogfish was sexed, and the total length (TL) and fork length (FL) were measured (±1 cm) by allowing the caudal fin to take a natural position. All animal lengths hereafter are TL. For those dogfishes with a damaged caudal fin, FL was converted to TL using TL = 1.08FL + 2.74 (n = 360, r^2 = 0.99). Dogfishes were weighed (±10 g) on a top-loading digital scale, and the relationship between weight and length was examined. Embryos were weighed to the nearest 0.1 g and length was measured to the nearest 0.1 cm.

Fig. 1. Topographic map of southeastern Australia indicating the six fishing locations where *Centroselachus crepidater* specimens were collected.

Spine preparation

Preliminary investigations found that the first dorsal-fin spines were more often damaged compared with the second dorsal-fin spines; therefore, second dorsal-fin spines were chosen for further examination. Second dorsal-fin spines were collected by cutting towards the vertebral column. Care was taken to include the delicate base portion. Spines were labelled and stored frozen for later examination.

Most of the muscle and connective tissue was removed from each spine using a sharp scalpel. Spine morphometrics (Fig. 2*a*) were measured using digital calipers (±0.01 mm). The external spine length (ESL) was measured from the tip of the spine to the point of entry into the flesh, and external spine width (ESW) was the diameter of the spine at this point of entry. Spines were thoroughly cleaned by repeatedly douching in hot tap water for a few seconds and then lightly scrapping with a blunt dental tool. Total spine length (TSL) was measured from the spine tip to the anterior side of the spine base. These morphometrics were used to examine spine

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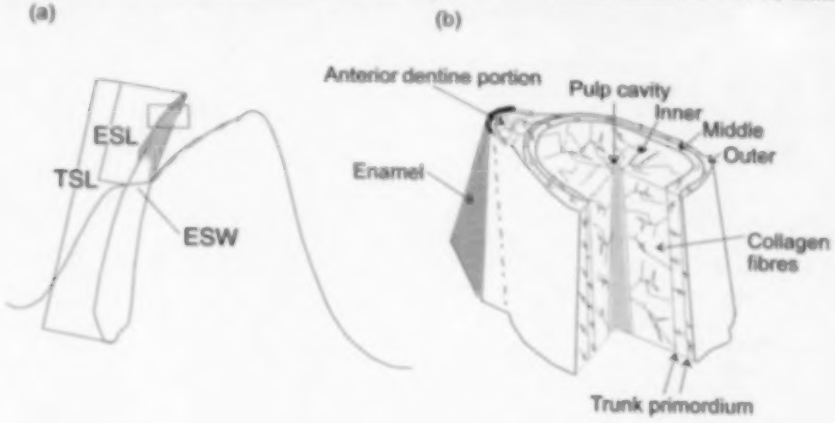
Fig. 2. (*a*) Dorsal fin spine illustrating morphometric measurements: total spine length (TSL), external spine length (ESL), and external spine width (ESW). (*b*) Internal structure of a dorsal-fin spine illustrating the three (inner, middle, and outer) dentine layers.



growth by investigating their relationship with animal size. Spines were kept wet or frozen until all external age analysis had been completed.

External base bands were enhanced by soaking in a solution of saturated alizarin red in 1% potassium hydroxide (KOH) at a ratio of 1:100 (1% *v/v*) for 3–5 days. After the first 24 h, the internal cartilage rod could be removed easily. Spines were rinsed in tap water and were either examined immediately or stored frozen. Band clarity could be increased by lightly polishing with wet fine-grade abrasive paper. All spines were examined under a low-power (6×) dissecting microscope, with a magnifying lamp, by the naked eye, or a combination of all three depending on the particular spine.

One external band describes either a ridge of enamel or a white band after rubbing a stained spine with wet abrasive paper. Counting started at the spine base and some spines showed better band clarity along the posterior edge. Staining did not always enhance bands on spines from younger or faster-growing fish, as the bands were widely spaced and ridges were less obvious. In some older fish, bands near the base were very tightly packed and could only be identified on the posterior margin of the spine.

On completion of all external band examination, the base of the spine was "plugged" with plasticine and placed laterally in Wonderflex® silicon cookware "brownie" molds and embedded in epoxy resin (Renlam M-1 AU resin and HY951 hardener at 9:1 *w/w*). Plugging the spine base prevented resin from moving into the pulp cavity, which could cause damage to the internal spine structure. About 5–15 transverse sections were taken from the tip of each spine using a lapidary saw (rpm = 1250) fitted with a diamond-tipped 0.6 mm wide blade. Section thickness was measured (±50 µm) with digital callipers and was generally 250–350 µm. The internal spine structure consists of three dentine layers: outer, middle, and inner (Fig. 2*b*). However, the internal dentine layer was much wider than the two other layers and had the clearest bands. The optimal sectioning point was immediately below the apex of the pulp cavity. Spine sections were mounted onto glass slides using epoxy resin. Slides were placed in a 35 °C oven until the resin had set (usually taking 1–2 h).

Bands are formed simultaneously in each of the three dentine layers (McFarlane and Beamish 1987). Band spacing is widest in the inner layer, and therefore, only bands in the inner dentine layer were counted. Counting started at the pulp cavity (spine centre) and continued outwards until the first trunk primordium (the junction between the inner and middle layers). One internal growth band refers to a dark (opaque) and light (translucent) concentric band.

Reading precision and accuracy

Three nonconsecutive band counts were made for each spine without prior knowledge of the animal's length or sex or the previous band counts. A subjective measure of band readability was used: the sliding scale started at 1 (samples with unambiguous bands with excellent readability) to 5 (unreadable sample). An independent reader was not available, and therefore, approximately 20% of the samples were re-examined 1–3 months after the first examination to imitate the second (independent) reader protocol suggested by Cailliet and Goldman (2004).

Precision was calculated using the coefficient of variance (CV) across all fish ages following Campana (2001). Calculating CV gave an assessment of the ease of ageing dogfish spines and tested the within-reader reproducibility of age determinations. Samples were discarded if the readability score was >3, and an upper limit for CV was set at 20% for each spine section (adapted from the index of average percent error (IAPE) for vertebrae analysis; Beamish and Fournier 1981). Samples were not included in the analysis if the CV was >20%. The average of the mean age for each of the three counts defined the age estimate for each shark (Casey et al. 1985).

Verification

The annual periodicity of internal bands was investigated by edge analysis and marginal increment analysis. An edge-grading system adapted from Yudin and Cailliet (1990) was applied for edge analysis. The condition of the growing edge of the inner dentine was examined under 60× to 100× magnification and was related to the season of capture. Edges

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were recorded as translucent, narrow opaque, or wide opaque. The observed and expected ratios of translucent to opaque last bands for each season were then compared using chi-square (χ^2) tests.

The marginal increment ratio (MIR) was calculated from transverse spine sections with 16–19 internal bands, where the width of the ultimate band (w_b) was expressed as a proportion of the penultimate band (w_{b-1}). All measurements (μm) were made using the F-View Soft Imaging System (SIS, 8 Timbertop Crt., Gulfview Heights, SA 5109, Australia; www.soft-imaging.net) on a BX51 Olympus compound microscope with a differential interference contrast. The radius of the inner dentine section was used to ensure that sections from the same regions were examined. Measuring the marginal increment in the inner dentine was difficult. Extremely thin (<300 μm) sections were required to ensure that the depth of field was minimised at high magnification. Mean MIR ± 1 standard error (SE) was plotted seasonally to locate periodic trends in band formation. If the translucent zones are formed annually, the MIR should decline once each year (i.e., when the new opaque zone starts to form outside the translucent zone). Analysis of variance (ANOVA) was performed to detect any significant differences in the MIR throughout the year.

The length-at-age data and growth curves were compared with published ages from radiometric isotope analysis of vertebrae for five female *C. crepidater* from southern Australia (Fenton 2001).

Growth

The von Bertalanffy growth model (VBGM) is commonly use to represent fish growth, although it does not always provide a particularly good fit and there has been a wide array of criticisms (Haddon 2001). Moulton et al. (1992) adopted the Francis (1988) reparameterized VBGM equation (eq. 1) for shark age and growth analysis to correct for the effects of gillnet length-selective sampling bias. The reparameterized equation was subsequently used to test for the biasing effects of gillnet length-selective fishing mortality (Walker et al. 1998):

$$(1) \qquad L = l_\phi + (l_\psi - l_\phi)(1 - r^{2(T-\phi)/(\psi-\phi)})/(1 - r^2)$$

where the three von Bertalanffy (1938) parameters (L_∞, t_0, and k) are replaced with l_ϕ (mean length at reference age ϕ), l_ψ (mean length at reference age ψ), l_2 (mean length at reference age $(\phi + \psi)/2$)), and $r = (l_\psi - l_2)/(l_2 - l_\phi)$. The same reference ages (ϕ and ψ) were chosen for males and females within the range of the data to avoid unnecessary extrapolations and to allow direct comparisons between male and female growth.

The Francis model was used to examine growth for each sex, and the Francis parameters were related to the conventional von Bertalanffy parameters using

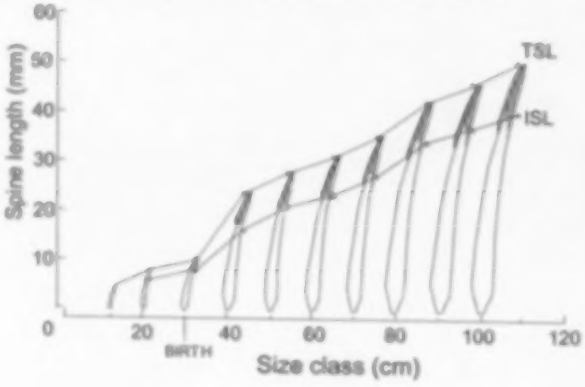
$$(2) \qquad L_\infty = l_\phi + (l_\psi - l_\phi)/(1 - r^2)$$

$$(3) \qquad k = -(2 \log_e r)/(\psi - \phi)$$

$$(4) \qquad t_0 = \phi + (1/k) \log_e((L_\infty - l_\phi)/L_\infty)$$

Confidence intervals (95%) around the Francis parameters gave a direct measure of the heterogeneity in length at age. Confidence intervals for both Francis and VBGM parameters were calculated using the nonlinear regression function in Systat 8.0® (Systat Software Inc. 1999).

Fig. 3. Relationship between animal size and mean second dorsal-fin spine length (total spine length, TSL; internal spine length, ISL) for male *Centroselachus crepidater* from southeastern Australia. (Shaded portions indicate spine pigmentation; see Fig. 4.)



Francis growth parameters were directly compared, although χ^2 tests on each likelihood ratio were used to compare the data between sex and external versus internal band counts. This method, advocated by Kimura (1980), Moulton et al. (1992), and Haddon (2001), is a more reliable means of finding a difference in growth. Chi-squared tests were performed in Microsoft Excel® as outlined by Haddon (2001).

The relationship between external and internal band counts was investigated by regression analysis using the nonlinear (mode/loss) regression function in Systat 8.0® (Systat Software Inc. 1999).

Longevity

Longevity was assumed to be the maximum number of external band counts.

Age at maturity

Sexual maturity in males was determined by clasper condition (elongation and calcification) and macro-examination of the testes. Males were considered mature once claspers had fully calcified and testes showed signs of lobulation. The reproductive status of females was based on the condition of the ovaries and uteri adapted from Wetherbee (1996) and Stehmann (2002). Females were assumed in a mature condition when distinct oocytes were present in the ovaries and (or) the uteri had expanded away from the central axis of the body cavity.

The age at maturity (A_{50}) was estimated from the relationship between the proportions of mature versus immature specimens within 5-year age classes. Each interval was indicated by its lower value. A logistic curve was fitted for each sex using probit analyses.

Results

The relationship between weight (W) and total length (TL) differed significantly with sex ($p < 0.05$): male, $W = 0.001\ TL^{3.434}$ ($r^2 = 0.67$, $n = 154$); female, $W = 0.002\ TL^{3.234}$ ($r^2 = 0.86$, $n = 238$). Length ranges were 30–79 cm for

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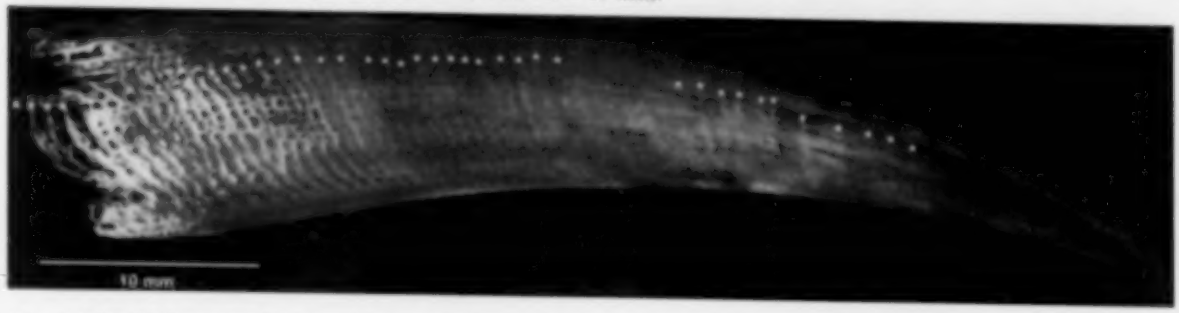
Fig. 4. Second dorsal-fin spine of *Centroselachus crepidater* stained with alizarin red and potassium hydroxide to enhance the external banding pattern (each asterisk (*) represents one band; scale bar = 10 mm).



males and 29–99.5 cm for females. The length frequencies indicate sexual dimorphism, with females attaining a larger size.

Spine structure and growth

The first and second dorsal-fin spines of *C. crepidater* are similar in size and structure. Each spine is slightly curved and the portion beneath the skin is ivory in colour, whereas the external portion is usually dark brown. A small strip of enamel covers the anterior dentine portion, and no other enamel is present on the spine surface. The cartilage rod that supports the spine is about two-thirds of the total spine length.

Spines were visible in embryos >10 cm TL, and full-term embryos (~30 cm TL) had fully developed spines measuring 8–9 mm TSL. A total of 344 second dorsal-fin spines were collected and measured, of which 267 had no damage, 55 had a worn or blunt tip, 18 had a broken tip, and four were broken and therefore discarded. The relationship between TL and TSL for nondamaged spines was linear and differed significantly between sexes ($p < 0.05$, $F = 9.98$): male, TL = 1.60 TSL + 16.02 ($r^2 = 0.67$, $n = 113$); female, TL = 1.12 TSL + 29.44 ($r^2 = 0.59$, $n = 142$).

Approximately 75% of the spine was beneath the skin. Spine growth was most rapid between 30 cm (birth) and 40 cm TL (Fig. 3), and the linear correlation strengthened significantly ($r^2 = 0.99$) after 40 cm TL for both sexes.

External bands

The external surfaces of 257 second dorsal-fin spines were examined for growth bands. A countable banding pattern (Fig. 4) was found on the surface of 241 (94%) spines. Overstaining was the main cause of poor readability, and most spines had a readability score of 1 or 2. The average reading precision (CV) of readable counts was 4.04%. Ten ages had a CV above 20% and were excluded from all age analyses. The number of bands did not influence readability, and there was very poor correlation ($r^2 = 0.054$, $n = 229$) between the number of bands and the coefficient of variance.

The number of external bands increased with animal size, and no bands were found close to the spine tip. The greatest number of bands observed was 54 (99 cm TL) for females and 34 (70 cm TL) for males. The largest female (99.5 cm TL) had 37 bands, and the largest male (79 cm TL) had 26 bands. Near-term embryos had no external bands, and a birth-band subtraction to estimate age was not required. The

Fig. 5. Reparameterized von Bertalanffy growth (VBG) curves generated from (*a*) external spine data for male (M, solid circles, $n = 86$) and female (F, open circles, $n = 146$) and (*b*) internal spine data for male (M, solid circles, $n = 69$) and female (F, open circles, $n = 100$) *Centroselachus crepidater* from southeastern Australia. Individual VBG and Francis parameters are given in Table 1.

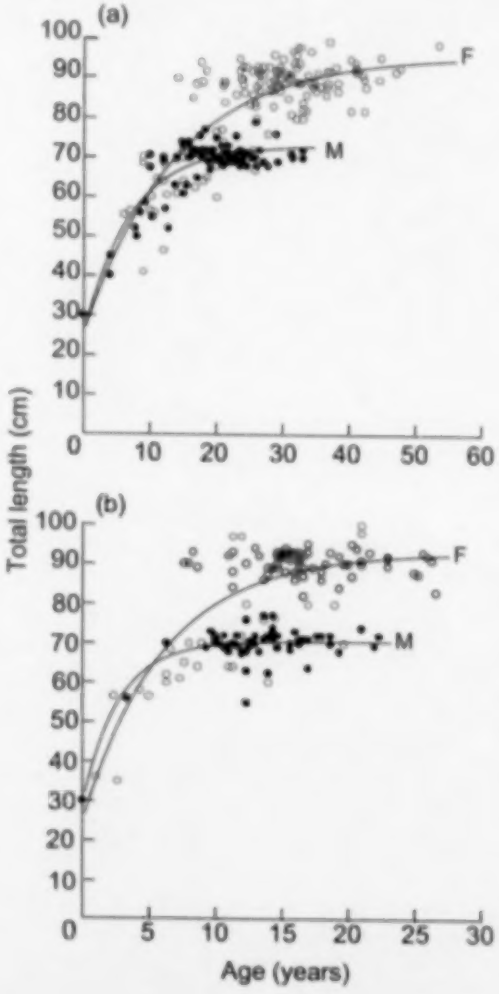


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Table 1. Estimates of the von Bertalanffy (1938) and Francis (1988) growth parameters (including upper and lower 95% confidence limits) for male and female *Centroselachus crepidater* from southern Australia.

Parameter		External bands		Internal bands	
		Male (n = 86)	Female (n = 146)	Male (n = 69)	Female (n = 100)
von Bertalanffy					
L_∞ (cm)	Estimate	73.2	96.1	70.6	93.2
	Upper	75.2	100.9	71.8	97.4
	Lower	71.2	91.6	69.3	88.9
k (year^{-1})	Estimate	0.141	0.072	0.362	0.163
	Upper	0.173	0.092	0.509	0.211
	Lower	0.109	0.052	0.215	0.116
t_0 (year)	Estimate	–2.99	–6.13	–1.51	–1.92
	Upper	–1.49	–4.59	–0.66	–0.49
	Lower	–4.47	–8.17	–2.36	–3.34
Francis					
l_2 (cm)	Estimate	37.6	42.6	50.8	45.9
	Upper	41.9	54.1	56.2	52.7
	Lower	33.2	31.1	45.3	39.1
l_{12} (cm)	Estimate	69.1	82.3	70.1	85.4
	Upper	69.9	85.4	71.0	97.3
	Lower	68.3	79.2	69.1	88.9
l_{22} (cm)	Estimate	73.2	96.3	70.6	93.2
	Upper	75.2	100.9	71.8	97.4
	Lower	71.2	91.6	69.3	88.9
r^2		0.75	0.78	0.73	0.66

Note: L_∞, asymptotic length; k, growth coefficient; t_0, age at length 0; r^2, coefficient of determination; l_2, mean total length (TL) at age 2; l_{12}, mean TL at age 12; l_{22}, mean TL at age 22.

base of larger (older) spines was fragile and was often only partly formed.

Assuming external bands are formed annually, the re-parameterized VBGM was fitted to length-at-age data for each sex (Fig. 5*a*; parameters are listed in Table 1). The Francis parameters show that males grow about 32 cm from the ages of 2 to 12, whereas females grow 40 cm over the same period. However, males only grew a further 4 cm over the next 10 years (between 12 and 22 years) compared with 14 cm for females.

Kimura's likelihood ratio test calculated a difference in the growth curves for male and female *C. crepidater*. A strong difference between the L_∞ of each sex was indicated (p = 0.009), whereas there was no indication that the t_0 and k parameters differed significantly (p = 0.569 and 0.122, respectively).

The number of external bands ranged from 0 to 54 years for females and from 0 to 33 years for males. However, most females were 24–34 years, whereas males 16–24 years were more common.

Internal bands

Cross sections of 201 spines were examined, and the inner dentine layer contained the most distinguishable banding pattern (Fig. 6). The optimal sectioning location (where band clarity was the best) was where the inner dentine was the widest; this corresponded to a region ~5 mm from the tip in unworn adult spines. Sections close to the tip had poor band clarity and the middle to outer layers were very narrow.

The number of internal bands increased with animal size, and the greatest number of bands observed was 27 (83 cm TL) for females and 22 (72 cm TL) for males. The spines of the largest female (99.5 cm TL) and male (79 cm TL) examined had unreadable internal bands. The largest female with readable internal bands (93 cm TL) had 21 bands, whereas the largest male with readable bands (77 cm TL) had 14 bands.

The mean CV of these bands was 7.7%, and 32 spines (15%) were excluded because of poor readability or poor

Fig. 6. Inner dentine layer from the spine of an 83 cm female *Centroselachus crepidater* with 25 bands. Measurements (μm) for marginal increment analysis: W_b, width of the last band; W_{b-1}, penultimate band width. Inner layer radius = 362 μm.

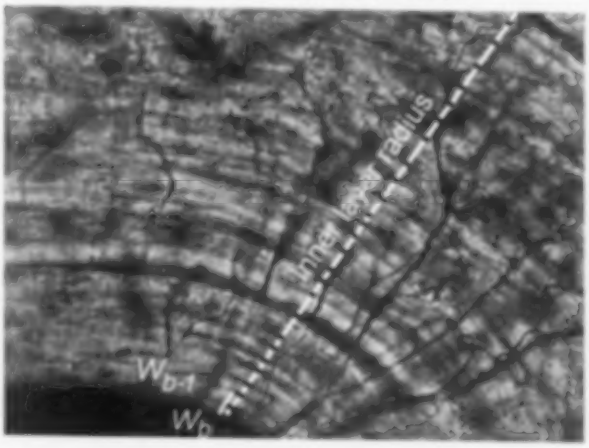

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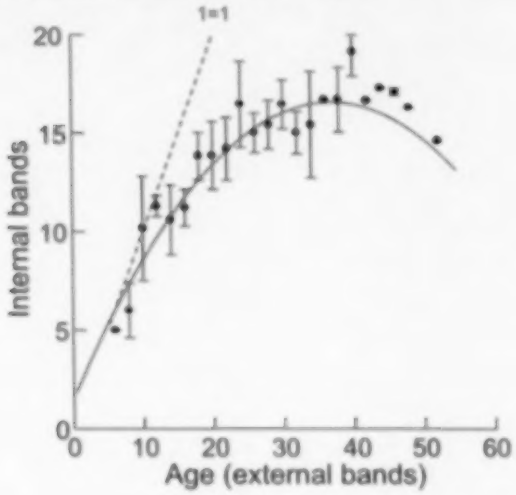
Fig. 7. Relationship between external bands (EB) and internal bands (IB). Plots are means, and error bars represent ±1 standard error. The polynomial relationship was IB = –0.011(EB^2) + 0.813(EB) + 1.552 (r^2 = 0.918, n = 111). Broken line indicates the exponential relationship if 1 EB = 1 IB.



reading precision (CV > 20%). A readability score of 2 was the most common. Near-term embryos had poor inner spine structure, and no bands were found in the dentine layers of embryos, making birth-band subtractions unnecessary.

The reparameterized VBGM was fitted to internal spine age data (Fig. 5*b*; the parameters are listed in Table 1). The Francis parameters indicated that females grew faster than males. Males grew 20 cm between the formation of 10 internal bands (between bands 2 and 12) compared with 40 cm for females. Over the next 10 bands (12 to 22 bands), males only grew by 1 cm compared with 6 cm for females.

Kimura's test found a strong difference between the L_∞ of each sex ($p < 0.001$), whereas there was only a slight difference between the k parameters of each sex ($p = 0.034$).

The number of internal bands (ages) ranged from 0 to 27 for females and from 0 to 22 for males. Most of the females collected had 8–16 internal bands, whereas males with 10–16 internal bands were more commonly collected.

Correlation between external and internal growth bands

A strong curvilinear relationship (r^2 = 0.936) was found between the number of external and internal bands (Fig. 7), with the number of external bands exceeding internal bands in most samples. The polynomial relationship showed that the first five bands were deposited at the same rate. However, over the next 10 years (external band ages 5 to 15), only one internal band was deposited for every 1.25 external bands. After 15 years, this rate rapidly declined, and after the age of 30, no new internal bands were deposited.

The growth curves from external bands were significantly different to the growth curves from internal bands. Francis parameters greatly differed for males, and Kimura's likelihood ratio test calculated a difference in the VBGM k parameter for each sex (male p = 0.023; female p = 0.015), whereas L_∞ also differed between the curves for males (p = 0.007).

Verification

The inner dentine layer of samples collected in spring had more wide opaque marginal edges than other edges (Fig. 8*a*), although a trend of annual band deposition could not be confirmed χ^2_3 = 1.32 (NS). A high mean MI ratio was calculated for each season (Fig. 8*b*), and MI did not differ significantly between seasons (ANOVA, df = 3, F = 0.744, p = 0.538). The small number of readable spine sections with 16–19 bands (n = 30) limited the use of marginal increment analysis, and both edge and marginal increment analyses failed to confirm a distinct seasonal pattern in band deposition.

The radiometric ages presented in Fenton (2001) were similar to the external band age estimates from this study (Fig. 9). There was no significant difference between the length-at-age data from external bands and radiometric age data from vertebrae (ANOVA, p = 0.31, F = 1.07).

Longevity

Based on the maximum number of external bands (A_{max}), female *C. crepidater* live about 20 years longer than males; the oldest male examined was 34 years old and oldest female was 54 years old.

Age at maturity

External band counts indicate that females mature (A_{50}) at about 20 years (SE = 0.5) (Fig. 10); this is 37% of A_{max}. Maturity occurred over a very broad age range (12–42 years), although the youngest female in the early stages of pregnancy (fertilised eggs in utero) was 27 years old, whereas the youngest pregnant female with near-term embryos was 29 years old.

Females matured over a wider age range than males. External band counts indicate that male maturity occurred over an 8-year period, the youngest mature male was 9 years old, and the oldest immature male was 17 years old. Male A_{50} was estimated to occur at the age of ~9 years (SE = 1.4) (Fig. 10), which is 26% of A_{max}.

Discussion

Dorsal spines affect the hydrodynamics of the dorsal fin and offer a degree of protection from predation (Maisey 1979). *Centroselachus crepidater* embryos have fully formed spines, although most of the spine is beneath the skin. After birth, external spine growth is rapid. A smaller external spine in utero may reduce the risk of injury to both mother and siblings, whereas a larger spine after birth may have a defensive and locomotory function.

Growth increments

The relationship between animal length and spine length suggests that *C. crepidater* spines continue to grow throughout life, making them a suitable structure for estimating age and investigating growth. Internal bands, similar to those reported by Tanaka (1990), were found in spine cross sections. However, external bands proved to be an alternative (and probably more accurate) method to estimate age.

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Fig. 8. (*a*) Proportion of edge type (solid diamonds, translucent; open squares, wide opaque; solid circles, narrow opaque) per season for both sexes combined. (*b*) Mean seasonal marginal increment (±1 standard error) for the inner dentine layer of *Centroselachus crepidater* second dorsal-fin spines with 16–19 opaque zones (n = 30).

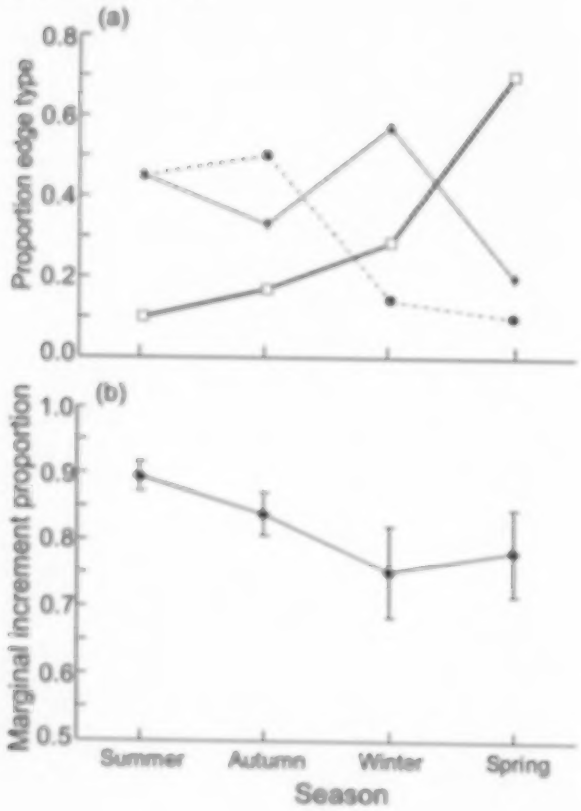


Fig. 9. Reparameterized von Bertalanffy growth curve generated from external spine data (solid circles) for female *Centroselachus crepidater* from southern Australia. Absolute age (×) from Fenton (2001), error bars represent error from radiometric technique. Growth curve generated from internal spine data (broken line) is included for comparison.

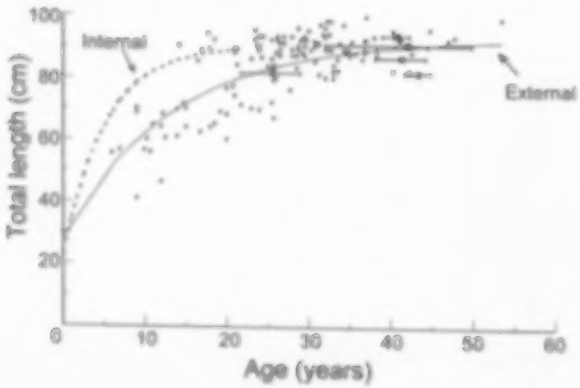
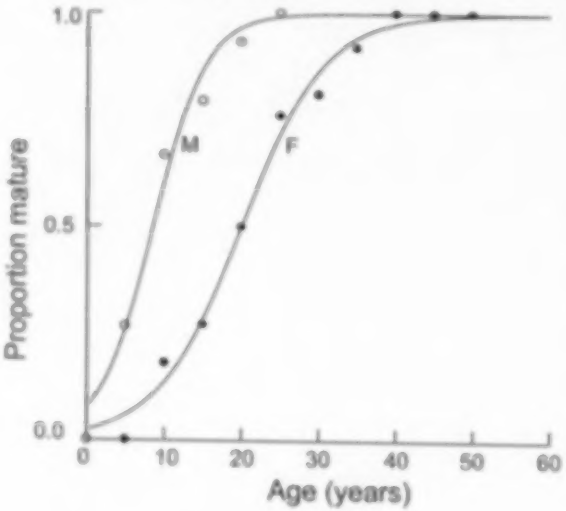


Fig. 10. Age at maturity ogives based on external band data for *Centroselachus crepidater* from southeastern Australia: male (M, open circles), n = 84, $P_A = 1/(1 + e^{(-\ln(19)(AGE-8.7)/(15.0-8.7))})$, r^2 = 0.99; female (F, solid circles), n = 137, $P_A = 1/(1 + e^{(-\ln(19)(AGE-19.8)/(35.0-19.8))})$, r^2 = 0.99.



Holden and Meadows (1962) overlooked the external bands on *S. acanthias* spines because of the ease of counting enamel bands. Maisey (1979) examined the structure and function of selachian fin spines and reported faint growth lines at the spine base of squalid (*Squalus*, *Etmopterus*, and *Deania* species) and heterodontid spines. External bands have also been noted on the spines of *Centroscymnus owstoni*, *Centrophorus uyato*, *Centrophorus squamosus*, *Deania calcea*, *Deania quadrispinosa*, *Etmopterus baxteri*, *Etmopterus* sp. B (Last and Stevens 1994), *Etmopterus lucifer*, *Etmopterus pusillus*, *Oxynotus bruniensis*, *Proscymnodon plunketi*, *Squalus megalops*, and *Heterodontus portusjacksoni* from southeastern Australia (S. Irvine, personal observation). These observations suggest that external bands on the spine may be suitable for ageing numerous shark species, and their usefulness in estimating age should be examined in future age and growth studies. Staining may not be necessary or beneficial for some spines (e.g., alizarin red only superficially stains *Deania calcea* spines and this stain decreased the band readability; S. Irvine, personal observation).

Both internal and external bands increased in number with animal length, although most spines had more external bands. The relationship between internal and external counts suggests that bands only formed at the same rate in the first 5 years. Internal band formation dramatically declined after 20 external bands had formed, and internal bands cease to form after 30 years (based on external bands). Maisey (1979) could not find a venous return system in adult spines and suggested that the inside of adult spines stop growing when the space above the pulp cavity has been filled by dentine. As spine growth rate slowed, the inner bands became more narrowly spaced in larger and (or) older animals. External bands also become more tightly packed, and larger and (or) older animals had spine bases with very little

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dentine. However, the number of external bands did not affect spine readability or reading precision.

Soldat (1982) and Nammack et al. (1985) used different growth areas of the spine to investigate the age of *S. acanthias* from the Northwest Atlantic. Soldat counted the internal bands in spine cross sections and obtained maximum ages of 20 (males) and 26 (females) years, while Nammack et al. used the enamel cap bands and reported maximum ages of 35 (males) and 40 (females) years. Nammack et al. suggested that the difference might be due to internal bands being grouped together as annuli during counting by Soldat. However, the growth curves predicted by these studies are remarkably similar, and internal and external bands were counted at a similar rate until 20 internal bands; internal bands then ceased to form at the same rate as external bands. Beamish and McFarlane (1985) validated the periodicity of enamel cap bands on *S. acanthias* from the Northeast Pacific through mark and recapture with tetracycline injection. A tetracycline mark was observed on the enamel, at the spine base, and within the inner dentine layer, and it was assumed that internal dentine bands were also annual. However, this assumption requires verification across all age and size ranges, as internal bands may not form annually in spines of older *S. acanthias*.

Precision and verification

The precision of the age data as indicated by the CV values showed that external bands were easier to interpret than internal bands. External bands form because of the lack of synchrony in upward spine growth and the continuous production of dentine at the spine base. Investigating the periodicity of external bands was not attempted (by either edge or marginal increment analyses), as external bands are not deposited in the typical opaque or translucent band pattern. However, enamel and internal dentine bands may be suitable for either edge or marginal increment analysis.

Marginal increment analysis was attempted on spines with 16–19 internal bands. Guallart Furio (1998) suggested that increment analysis would be impossible on squalid spines, as obtaining sections from the same spine location is required. To ensure spine sections from a similar location were used for increment analysis, the diameter of the spine section and the inner layer radius were measured. Marginal increment analysis was attempted on the internal bands, although the periodicity of band formation was inconclusive because of the small number of animals collected in the appropriate age class each month or season. The high longevity of this species and the wide age range suggests that a very large ($n > 1400$) sample size would be required to accurately attempt either edge or marginal increment analysis on a single age class of *C. crepidater*. Verifying band periodicity in spines using marginal increment analysis or edge analysis is likely to remain problematic, especially when the study species have a high longevity or when samples are collected opportunistically over a limited sampling period.

The applicability of independent ageing techniques (including radiometric analysis and radiobomb carbon dating) on the dorsal-fin spine also deserves further attention. External spine age estimates for female *C. crepidater* were comparable with the absolute ages of five large females estimated by radiometric analysis from vertebrae (Fenton 2001). The results of Fenton (2001) are based on many assumptions, and Welden et al. (1987) suggested that elasmobranch vertebrae were unsuitable for radiometric analysis. However, the similarity between the two data sets indicated that further research into radiometric ageing of shark vertebrae is required.

McFarlane and Beamish (1987) reported the incorporation of tetracycline into *S. acanthias* spines, making them a suitable structure to age after chemical tagging. However, very little is known about the survivability rate or chance of recapture of deepwater sharks. Yano and Tanaka (1986) successfully tagged and tracked two deepwater dogfishes (*Centrophorus acus*) caught by dropline, although this tracking study was abandoned after 24 h. Deepwater sharks may therefore survive being brought to surface waters to allow conventional tagging and tetracycline injection for ageing purposes.

Growth

The cue for growth (and therefore band deposition) in the deep sea is unknown. An annual cycle in food quantity and quality is often assumed (Clarke 2000; Swan and Gordon 2001), although seasonal dietary changes have not been investigated for deepwater dogfishes. Off southern Tasmania, there is no seasonal change in the species composition for the more abundant species, although micronekton composition does vary seasonally (Williams and Koslow 1997). This suggests that, if a change in diet is the cue for growth, it may be an increase in prey abundance (quantity) rather than a change in prey species (quality).

The Francis (1988) reparameterized von Bertalanffy growth model fits the observed length-at-age data well. Male and female growth was similar until males became mature. Males matured (A_{50}) at about 9 years, whereas females matured at about 20 years. However, maturity analysis required samples to be put into age classes represented by their lower values; age at maturity may therefore best be indicated over an age range.

Maturity

The estimated age at maturity differed from the age at maternity (the youngest pregnant female). Females matured at about 20 years, although the age of youngest female with candled uteri (early pregnancy) was 27 years and the age of the youngest female with near-term embryos was 29 years. Walker (2004) suggested the use of a maternity ogive rather than a maturity ogive for estimating recruitment in population dynamic models.

However, this becomes difficult for species that have an unknown gestation period and resting stage between pregnancies. There is no difference in the size at maturity (L_{50}) and the size of the smallest pregnant female (both 82 cm TL) (S. Irvine, unpublished data), suggesting that females might not grow during reproductive activity. Further growth may only occur during the resting period (between pregnancy and next follicle development phase).

Productivity

Centroselachus crepidater from southeastern Australia exhibits slower growth (Fig. 11) and higher longevity than most other dogfish species. However, *C. squamosus* from the Northeast Atlantic has a longevity of 70 years (Clarke et al.

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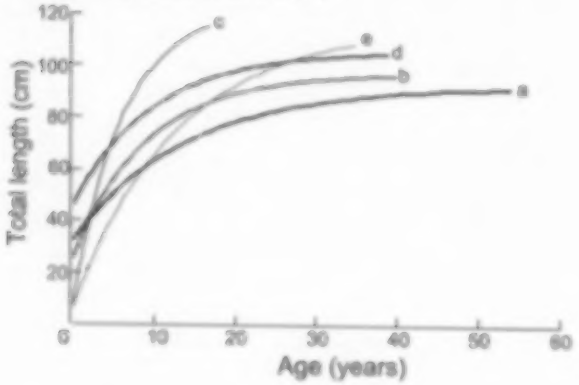
Fig. 11. Various von Bertalanffy growth curves for female dogfish species: a, *Centroselachus crepidater*, this study; b, *Squalus acanthias*, Nammack et al. (1985); c, *Centrophorus acus*, Tanaka (1990); d, *Centrophorus granulosus*, Guallart Furio (1998); e, *Deania calcea*, Clarke et al. (2002*b*).



2002*a*) and remains the oldest dogfish species ever aged (albeit unvalidated).

Centroselachus crepidater from southeastern Australia has a mean litter size of six and the reproductive cycle is noncontinuous with no seasonal trend (Daley et al. 2002). Although the length of gestation is unknown, it seems reasonable to assume that the reproductive cycle (follicle development and gestation and resting period) would exceed 1 year and is probably 2 or more years. If a cycle of 2 years were assumed, an annual fecundity of three would indicate a maximum productivity of 102 offspring per lifetime. However, if the cycle were 3 years, then the maximum productivity would only be 68 offspring per lifetime.

The resilience of a species to fishing pressure depends on vulnerability to the fishing gear and biological productivity (Stevens et al. 2000). The high longevity and late age at maturity of *C. crepidater* from southeastern Australia are indicators of low productivity. Smith et al. (1998) assessed the productivity of 26 shark species using published age at maturity and maximum reproductive age data. According to this rank of sensitivity to fishing pressure, *C. crepidater* has a lower recovery capability than all of the Pacific shark species examined by Smith et al.

Nonselective trawl fishing off southeastern Australia collected a wide age range of *C. crepidater*, although most females had only recently matured (24–34 years old). The removal of this crucial component is likely to be unsustainable, and precautionary management regimes (including closed areas) need to be implemented immediately to avoid local extirpations. In light of this new information on age and growth, international management and conservation attention need to be directed towards dogfishes.

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An evaluation of stable nitrogen isotopes and polychlorinated biphenyls as bioenergetic tracers in aquatic systems

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Abstract: This study investigated the relationship between stable nitrogen isotopes ($\delta^{15}N$) and polychlorinated biphenyl (PCB) concentrations in rock bass (*Ambloplites rupestris*) and bluegill sunfish (*Lepomis macrochirus*) with respect to age, size, and diet. $\delta^{15}N$ signatures in both species exhibited enrichment with increasing size and approached steady state with respect to dietary $\delta^{15}N$ values by the second year of growth. Young-of-the-year fish, however, exhibited lower nitrogen isotope enrichment over the diet, indicating that the commonly held trophic enrichment factor of 3.4‰ is more suitable for older, slow-growing individuals. PCB accumulation in both species progressed from being dominated by uptake from water in small (<100 g) fish to dietary uptake in larger individuals as a function of bioenergetic constraints such as food energy conversion and contaminant assimilation efficiencies. Significant increases in PCB accumulation were attributed to decreased specific growth rates such that ≤60% of body mass was gained on an annual basis. This effect was most noted in bluegills where higher PCB biomagnification factors were a consequence of increased foraging costs associated with an invertebrate diet. It is concluded that growth-related changes in species bioenergetics regulate both contaminant accumulation and $\delta^{15}N$ dynamics.

Résumé : Notre étude examine la relation entre les isotopes stables d'azote ($\delta^{15}N$) et les concentrations de biphényls polychlorés (« PCB ») chez le crapet de roche (*Ambloplites rupestris*) et le crapet arlequin (*Lepomis macrochirus*) en fonction de l'âge, de la taille et du régime alimentaire. Chez les deux espèces, les signatures de $\delta^{15}N$ accusent un enrichissement en fonction directe de la taille et elles s'approchent d'un état d'équilibre en regard des valeurs alimentaires de $\delta^{15}N$ durant la seconde année de croissance. Les jeunes poissons de l'année subissent un enrichissement moindre des isotopes d'azote en fonction du régime alimentaire, ce qui indique que le facteur d'enrichissement couramment utilisé de 3,4 ‰ est plus convenable pour les individus plus âgés à croissance plus lente. L'accumulation des PCB chez les deux espèces change d'une prédominance d'absorption à partir de l'eau chez les petits (<100 g) poissons à une absorption alimentaire chez les poissons plus grands en fonction des contraintes bioénergétiques, telles que les efficacités de la conversion énergétique des aliments et de l'assimilation des contaminants. Les accroissements significatifs de l'accumulation de PCB s'expliquent par la diminution des taux spécifiques de croissance de sorte que ≤60 % de la masse corporelle est ajouté chaque année. Cet effet est plus commun chez les crapets arlequins chez qui les facteurs plus élevés de bioaccumulation sont une conséquence des coûts plus grands de recherche de la nourriture associés à un régime alimentaire à base d'invertébrés. Nous concluons que les changements des relations bioénergétiques reliés à la croissance contrôlent tant l'accumulation des contaminants que la dynamique du $\delta^{15}N$.

[Traduit par la Rédaction]

Introduction

Stable nitrogen isotope signatures ($\delta^{15}N$) reflect the proportion of assimilated prey ingested over a period of time (Minagawa and Wada 1984) and therefore represent time-integrated measures of feeding relationships (Cabana and Rasmussen 1994). The establishment of animal trophic position and prey item proportions from $\delta^{15}N$ measured in multiple species sampled from a food web relies on the use of mixing models which generally assume that animal tissues are in steady state with their diet at the time of sampling (Ben-David and Schell 2001). Failure of this assumption, as will occur if an organism is sampled after a recent diet shift, can result in incorrect assignment of prey items and animal trophic position. Testing the steady-state assumption remains difficult because few kinetic studies have been conducted to determine the time required for stable isotopes in different species of fish, or within different tissues of a fish, to

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achieve steady state following diet shifts (Gannes et al. 1997; Olive et al. 2003).

Enrichment of ^{15}N within fish tissues over that of its diet arises as a result of the slightly greater retention of the heavier isotope over the lighter one (^{14}N) during nutrient assimilation and protein catabolism to produce steady-state $\delta^{15}N$ ratios in organism tissues that are approximately 3.4‰ higher than those in the diet (Minagawa and Wada 1984). Studies have demonstrated protein catabolism during starvation to enrich $\delta^{15}N$ (Hobson et al. 1993; Doucett et al. 1999), and recent kinetic models for stable isotopes have recognized the occurrence of separate assimilation and catabolism fractionation reactions (Olive et al. 2003). If the mechanisms of isotope fractionation differ between nitrogen assimilation/protein anabolism and protein catabolism, then the magnitude of the steady-state enrichment factor may differ between organisms exhibiting rapid growth (i.e., fractionation proceeding mainly by the assimilation/anabolism pathway) compared with animals approaching maintenance growth (i.e., fractionation proceeding mainly by the catabolic pathway). Models of this type predict changes in both the time to steady state and the magnitude of the trophic enrichment factor as a function of animal growth rates (Olive et al. 2003). The basis of the trophic enrichment factor of 3.4‰ remains an empirical observation (Olive et al. 2003), and little is understood about the actual metabolic pathways governing ^{15}N fractionation or how the kinetics of the fractionation process varies during protein synthesis and catabolism of individual proteins and tissues (Gannes et al. 1997).

Despite the above uncertainties, the more common modeling approach for stable isotopes assumes that trophic enrichment rates remain constant and that changes in isotope signatures resulting from diet shifts can be modeled as a function of growth rates and metabolic tissue replacement as outlined by Hesslein et al. (1993) below:

$$(1) \qquad C_{\delta(t)} = C_n + (C_o - C_n) \cdot e^{-(g+m)t}$$

This model assumes that isotope signatures in the animal have reached steady state with respect to the signature of the old diet (C_o) before a diet shift. However, the time required for tissues to reach steady state with the new diet (C_n) is driven by growth rates (g; day^{-1}) and metabolic tissue turnover (m; day^{-1}) (Hesslein et al. 1993). Under this consideration, eq. 1 can be modified to reflect such kinetics:

$$(2) \qquad C_{\delta(t)} = C_{\delta(ss)} + (C_{\delta(ss)} - C_{\delta(o)}) \cdot e^{-(g+m)t}$$

Equation 2 now accounts for deviations between stable isotope signatures realized in fish tissues at time (t) following a diet shift ($C_{\delta(t)}$) from the steady-state value ($C_{\delta(ss)}$) resulting from a failure of the organism to achieve steady state with the new diet at the time of sampling. For the stable isotope of nitrogen, the value for $C_{\delta(ss)}$ is estimated using the empirical trophic enrichment factor of 3.4‰ for (i.e., 3.4 + $C_{\delta(diet)}$; Minagawa and Wada 1984). Thus, the model of Hesslein et al. (1993) can be expressed as

$$(3) \qquad C_{\delta(t)} = C_{\delta(o)} + (\mathrm{ER} + C_{\delta(diet)} - C_{\delta(o)}) \cdot e^{-(g+m)t}$$

where ER is the enrichment rate of 3.4‰ expected for $\delta^{15}N$ and $C_{\delta(diet)}$ is the average $\delta^{15}N$ signature of the diet. The model suggests that stable isotope kinetics are driven by specific growth rates and will be maximized in rapidly growing animals (Hesslein et al. 1993). In contrast, fish that are approaching their maximum size exhibit slow growth and protein synthesis rates, with much of the amino acid pool supplied by metabolic turnover. According to the Hesslein et al. (1993) model, $\delta^{15}N$ signatures in these animals may take years to achieve steady state ($C_{\delta(ss)}$) following a diet shift.

Several studies have demonstrated strong correlations between $\delta^{15}N$ and persistent organic pollutant (POP) bioaccumulation within aquatic food webs (Cabana and Rasmussen 1994; Kidd et al. 1995; Kiriluk et al. 1995). As with stable isotopes, POPs can be accumulated in fish from food (Russell et al. 1999) and therefore may also serve as tracers of trophic structure (Rasmussen et al. 1990; Haffner et al. 1994) and animal bioenergetics when dietary uptake dominates the contaminant-exposure pathway (Madenjian et al. 1998; Paterson et al. 2005). Unlike stable isotopes, the mechanisms describing bioaccumulation kinetics for hydrophobic organic contaminants such as PCBs and dichlorodiphenyltrichloroethane (DDT) have been better defined experimentally. Contaminant bioaccumulation is primarily a function of the differences in the relative partitioning capacity among the animal, water, and its food and limitations in diffusion kinetics of chemical exchange across gill surfaces and between the animal and its gastrointestinal contents (Gobas et al. 1993). The *n*-octanol–water partition coefficient (K_{ow}) provides a surrogate measure of chemical hydrophobicity and has been shown to be an important predictor of bioaccumulation potential for POPs (Mackay 1982). In aquatic organisms, the primary route of exposure for less hydrophobic pollutants of $\log K_{ow} < 5$ is across the skin or gills (bioconcentration) (Clark et al. 1990). For more hydrophobic contaminants of $\log K_{ow} \sim 5$–7, uptake from food becomes the dominant path of exposure in larger, slow-growing animals (Thomann et al. 1992). For POPs, the degree of bioaccumulation and time to steady state are controlled by the kinetics of elimination (Morrison et al. 1999), with the higher $\log K_{ow}$ chemicals often demonstrating the phenomenon of biomagnification whereby the chemical potential in the animal exceeds that of its food or environment (Connolly and Pedersen 1988; Gobas et al. 1993). These more hydrophobic contaminants also demonstrate food web biomagnification where chemical potentials, approximated by expressing chemical concentrations on a lipid weight basis (Connolly and Pedersen 1988), exhibit average trophic enrichment on the order of 3–5 for each trophic position (Oliver and Niimi 1988). POP trophic enrichment factors have been mechanistically described as a function of changes in the volume and partition capacity of food along the gastrointestinal tract during digestion and assimilation (Gobas et al. 1988, 1993, 1999).

Empirically based kinetic models of POP accumulation are similar in structure to those for stable isotopes. A general model for contaminant uptake from water and food is described in eq. 4:

$$(4) \qquad C_{org(t)} = C_{org(o)} + \left[\left(\frac{k_1 C_w + k_g C_{food}}{k_2 + k_g}\right) - C_{org(o)}\right] \times (1 - e^{-(k_2 + k_g)t})$$

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where contaminant accumulation at time t following exposure ($C_{org(t)}$) is a function of the initial burden ($C_{org(t=0)}$) and chemical accumulation from water ($k_1 \cdot C_w$) and food ($k_d \cdot C_{food}$), where k_1 and k_d represent the chemical uptake rate constants from water and food, respectively. Depuration kinetics are represented by the rate constants for growth dilution (k_g) and the sum of chemical elimination through fecal egestion, metabolism, and across gill surfaces (k_2) (Mackay 1982; Morrison et al. 1997). Laboratory data have demonstrated that this model can be further simplified to include only water as an exposure route for chemicals having $\log K_{ow}$ in the range of 3–5 (Clark et al. 1990). For low K_{ow} chemicals, bioaccumulation is predicted according to

$$(5) \qquad C_{org(t)} = C_{org(t=0)} + (\mathrm{BCF} \cdot C_w - C_{org(t=0)}) \cdot (1 - e^{-(k_2 + k_g)t})$$

where the bioconcentration factor (BCF) is the ratio $k_1/(k_2 + k_g)$. For chemicals of $\log K_{ow} > \sim 5.5$, dietary uptake dominates the exposure pathway (Thomann et al. 1992) and the ratio $k_d/(k_2 + k_g)$ defines the biomagnification factor (BMF) allowing simplification of eq. 4 to

$$(6) \qquad C_{org(t)} = C_{org(t=0)} + (\mathrm{BMF} \cdot C_{food} - C_{org(t=0)}) \cdot (1 - e^{-(k_2 + k_g)t})$$

When modeling POPs, it is important to distinguish between the contributions of bioconcentration and biomagnification, as only the latter provides information regarding animal trophic position. As with stable isotopes, the time to steady state of POP accumulation, for both bioconcentration and biomagnification, is a function of organism bioenergetics and growth rates. At steady state, chemical uptake from food and water is balanced by elimination through fecal egestion, metabolic transformation, and losses across respiratory surfaces in addition to growth dilution (Morrison et al. 1997). Growth (Moreau 1987) and chemical elimination rates (Trudel and Rasmussen 1997) are negatively correlated with body size, and therefore, extended time frames are predicted for large, slow-growing animals to achieve steady state. Additionally, the transition in chemical accumulation from bioconcentration to biomagnification kinetics in such organisms will depend on body mass such that larger animals are predicted to biomagnify chemicals of lower $\log K_{ow}$ than smaller, rapidly growing species with relatively higher k_2 and k_g rate constants. For stable isotopes, however, high growth rates are hypothesized to stimulate faster isotope accumulation kinetics (Hesslein et al. 1993). Therefore, stable isotopes and POPs are independent measures of ecological structure, but the mechanisms regulating tissue retention and elimination differ substantially for these ecological descriptors.

Under these considerations, combined studies on contaminant and stable isotope accumulation will provide improved confidence in model-assigned trophic positioning of organisms within a given food web, particularly when organisms are subject to omnivory (Vander Zanden et al. 2000) or have recently exhibited ontogenetic diet shifts. Studying stable isotope and POP accumulation in early and juvenile life stages of fish provides an ideal system in which to test these relationships because of the tendency of fish to undergo both ontogenetic diet shifts and substantial changes in growth rates during this life history period (Werner and Gilliam 1984; Mittelbach and Persson 1998).

In this study, rock bass (*Ambloplites rupestris*) and bluegill sunfish (*Lepomis macrochirus*) were collected from the Detroit River to quantify ontogenetic-related changes in stable isotope enrichment and chemical accumulation. The objectives of this study are (*i*) to quantify relationships between chemical accumulation and stable isotope enrichment as functions of ontogenetic diet shifts and growth and (*ii*) to compare chemical concentrations in small, rapidly growing fish with those in larger, older individuals to determine the body size at which chemical accumulation kinetics switch from water-based bioconcentration kinetics to a dietary, bioaccumulation uptake process.

Materials and methods

Rock bass and bluegill sunfish were collected using a benthic trawl net towed behind a research vessel near the confluence of Lake St. Clair and the Detroit River in October of 2001. Specimens for chemical and stable isotope analyses were wrapped in solvent (hexane) rinsed aluminum foil, stored at 4 °C, and transported to the laboratory for collection of biological data. An additional sample of the smallest rock bass was preserved for gut content analysis in a 10% formalin solution. For bluegills, gut contents were identified from the frozen specimens before preparation for organic pollutant extraction. Upon return to the laboratory, biological data including total length, fork length, and weight were measured.

Age determination was completed using sagittal otoliths removed from frozen individuals following procedures outlined by the Otolith Research Laboratory, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada. Difficulty in reading otolith annuli for rock bass > 4 years old required use of life history tables (Scott and Crossman 1973) along with additional literature-based length-at-age ranges for this species (Putman et al. 1995). Specific growth rates (%·day^{-1}) were calculated for each age class using the following equation (Ricker 1979):

$$(7) \qquad [\ln(W_t/W_0)/t] \times 100$$

where W_0 was the average weight (grams) of the initial year class, W_t was the average weight of the next year class, and t was the length of the growing period in days. Initial weights for the young-of-the-year (YOY) age class were taken from the intercepts of the length vs. weight regression plots with a day 0 value of 1 June used for this age class.

PCB analysis

Following collection of biological data, individual fish >5 g in size were homogenized using a solvent-rinsed stainless steel blender. For YOY fish with body mass <5 g, at least three fish were pooled to generate sufficient material for chemical analysis, with five pooled samples analysed for this age class in both species. Full details of the extraction and analysis protocols are outlined in O'Rourke et al. (2004). Briefly, approximately 5 g of the whole-body homogenate was added to 25 g sodium sulfate and the mixture was cold column extracted for 1 h in a 50:50 hexane–dichloromethane solution. Lipid fractions were removed via gel permeation

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Table 1. Dietary polychlorinated biphenyl (PCB) congener concentrations and elimination rate constants (k_2) used in PCB bioaccumulation model (eq. 6) for rock bass (*Ambloplites rupestris*) and bluegills (*Lepomis macrochirus*).

Species	Age class	Dietary concentrations[a] (10^{-2} μg·g^{-1} (lipid))			Elimination rate constants[b] (10^{-2} day^{-1})			Biomagnification factors[c]		
		PCB 28	PCB 52	PCB 153	PCB 28	PCB 52	PCB 153	PCB 28	PCB 52	PCB 153
Rock bass	YOY	0.6	2.0	1.4	2.6	1.8	0.5	1.8	3.3	9.3
	1	0.6	2.0	1.7	0.7	0.5	0.1	2.8	3.9	12.6
	2	0.8	2.8	3.1	0.3	0.2	<0.1	0.8	1.3	9.5
	4	2.1	10.0	10.1	0.1	<0.1	<0.1	2.7	4.2	14.7
	6	2.1	10.6	11.9	<0.1	<0.1	<0.1	1.8	1.9	10.3
	7	2.1	11.5	14.7	<0.1	<0.1	<0.1	2.4	4.8	13.4
Bluegills	YOY	0.6	2.0	0.4	1.2	0.8	0.2	1.2	0.7	7.6
	1	0.6	2.1	0.4	0.3	0.2	<0.1	2.0	1.4	10.0
	3	0.6	3.7	1.8	0.1	0.1	<0.1	1.6	3.0	30.5
	4	0.6	3.9	2.4	0.1	<0.1	<0.1	2.6	2.5	18.6
								2.1[d]	2.9[d]	16.0[d]

Note: YOY, young-of-the-year.

[a]Dietary PCB congener concentrations represent average levels estimated from PCB concentration data for benthic invertebrate and cyprinid forage fish species previously collected at sampling location (Great Lakes Institute for Environmental Research 2003).

[b]Elimination rate constant values allometrically scaled from those calculated for juvenile rainbow trout ~3 g in size (Fisk et al. 1998).

[c]Biomagnification factors calculated by solving eq. 6 for BMF (see Materials and methods).

[d]Biomagnification factors from Fisk et al. (1998) used for the calculation of PCB congener accumulation profiles.

chromatography, and lipid content was determined gravimetrically. Sample cleanup was completed using Florisil columns, and all chemical residue analyses were completed on a gas chromatograph (HP G1530A; Hewlett Packard Company, Palo Alto, California) equipped with a mass selective detector (HP 5973). Method blanks, an internal reference sample homogenate (carp), and a 1:1:1 mixture of Aroclor 1248–1252–1264 PCB standards were run on the gas chromatograph every five samples. Recoveries of surrogate standards averaged 83% ± 18% (standard deviation, SD). Tissue concentrations were not corrected for surrogate standard recoveries.

PCB accumulation profiles in rock bass and bluegill age classes were predicted for congeners 28, 52, and 153 using the model outlined in eq. 6. BMF and elimination rate constants (k_2) applied in the model were those determined by Fisk et al. (1998) (Table 1). Chemical elimination rate constants, however, have been demonstrated to be negatively correlated with body size (Trudel and Rasmussen 1997). Using the k_2 values as determined for these congeners in ~3 g rainbow trout (*Onchorynchus mykiss*) (Fisk et al. 1998) and the general allometric equation (aW^b), an exponent of –0.75 was substituted (Peters et al. 1996) and the relation was then solved for the constant. Subsequently, k_2 values for PCBs 28, 52, and 153 were allometrically scaled for each centrarchid size (age) class (Table 1). PCB congener concentrations in food (C_{food}) used in the model were representative of the ranges reported for benthic invertebrates and cyprinid forage fish previously collected from the sampling area (Table 1; Great Lakes Institute for Environmental Research 2003). Food concentrations were adjusted for each size class to reflect changes in dietary PCB burden as the fish grew. Specific growth rates determined for each size class of rock bass and bluegill (eq. 7) were used to estimate the growth rate dilution constants (k_g). Additionally, to determine potential changes in BMFs as fish grew in size, eq. 6 was solved for BMF using the measured concentrations of PCB congeners 28, 52, and 153 for $C_{organism}$ in each size class and their concentrations in food as described above (C_{food}).

Stable isotope analysis

Stable isotope analysis was completed using the pooled and individual-fish whole-body homogenates from each age class as generated for chemical analysis. Approximately 2 g of the whole-body homogenate was dried at 75 °C for 48 h and ground to a fine powder using a glass mortar and pestle (Vander Zanden et al. 2000). Between 0.8 and 1.1 mg of the dried powder was added to a 3 mm × 5.5 mm tin capsule, which was subsequently folded closed and placed in an individually labeled sample tray. All sample analyses were completed by the Environmental Isotope Laboratory at the University of Waterloo (Waterloo, Ontario, Canada) using a Micromass VG Isochrom continuous-flow stable isotope ratio mass spectrometer (Micromass UK Limited, Manchester, UK) coupled to a Carlo Erba elemental analyzer (Carlo Erba Instruments, Milan, Italy). Stable isotope results are calculated relative to a reference standard and expressed as delta (δ) notation as per eq. 6:

$$(8) \qquad \delta^{15}\text{N or } \delta^{13}\text{C } (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$. Nitrogen results were standardized against atmospheric N_2 with the analyses of International Atomic Energy Agency N1 and N2 (ammonium sulfates) and CH6 (sugar) standards also completed during evaluation of biological samples. Precision (±2 SD) of these internal standards is ±0.3‰ and ±0.2‰ for nitrogen and carbon, respectively, over several years of use. Duplicate analyses were also completed on 15% of the samples with variability estimates, reported as the standard error of the estimate, of 0.2‰ reported for δ^{15}N results.

Prey isotope signature calculation

To determine ER of δ^{15}N by rock bass and bluegill, we estimated prey δ^{15}N results for each year class of both species

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Table 2. Trophic positions and predicted stable nitrogen isotope signatures calculated for prey categories identified during gut contents analysis.

Prey category	Dietary trophic position[a]	Predicted $\delta^{15}N$ trophic position[b]	Predicted $\delta^{15}N$ (‰)	Reported $\delta^{15}N$ (‰)
Arachnida (water mites)	3.0	3.2	10.1	—
Cladocera	2.5	2.8	8.8	—
Copepoda	2.5	2.8	8.8	—
Amphipoda	2.5	2.8	8.8	5.1–9.1[c]
Trichoptera (caddisflies)	2.5	2.8	8.8	—
Diptera (chironomids)	2.5	2.8	8.8	—
Cyprinidae	2.5	2.8	8.8	9.8[d]–12[e]
Decapoda (crayfish)	3.0	3.2	10.1	—
Gastropoda (snails)	2.0	2.4	7.4	6[f]
Pelycypoda (zebra mussels)	2.0	2.4	7.4	7[f]
Detritus–other	1.0	1.6	4.8	4.1[c]

Note: Predicted prey $\delta^{15}N$ signatures were determined based on the solution of the $\delta^{15}N$ trophic calculation outlined in eq. 10.

[a]Dietary trophic positions are those for each prey category as presented in Vander Zanden et al. (1997).

[b]$\delta^{15}N$ trophic positions were predicted using the linear regression describing the relationship between dietary trophic position and $\delta^{15}N$ trophic position estimates (Vander Zanden et al. 1997).

[c]Limén et al. (2005).

[d]Hebert et al. (1999).

[e]Cabana and Rasmussen (1996).

[f]Mazak et al. (1997).

using the mixing model described in eq. 9 (Hart and Lovvorn 2002):

$$(9)\quad \delta^{15}N_{\text{mixed prey}} = [\%\text{diet}_1(\delta^{15}N_1) + \%\text{diet}_2(\delta^{15}N_2) + \ldots + \%\text{diet}_n(\delta^{15}N_n)] \times 100$$

where $\%\text{diet}_n$ is the percent of total diet items represented by the nth diet item and $\delta^{15}N_n$ is its isotope value. To determine prey item isotope signatures, prey items were assigned to a dietary trophic position as calculated by Vander Zanden et al. (1997) and then converted to $\delta^{15}N$ trophic positions using the linear regression describing the relationship between dietary and $\delta^{15}N$ trophic positions (Vander Zanden et al. 1997). The resultant $\delta^{15}N$ trophic positions for each prey item were then converted to $\delta^{15}N$ estimates based on reorganization of the $\delta^{15}N$ trophic position calculation (eq. 10) and solving for prey $\delta^{15}N$:

$$(10)\quad \text{Tropic position} = [(\text{prey } \delta^{15}N - \text{baseline } \delta^{15}N)/3.4] + 2$$

To calculate trophic position, correction of the prey $\delta^{15}N$ signature to that of a long-lived primary consumer has been recommended to account for potential background variability in nutrient loading (Cabana and Rasmussen 1996). To estimate a baseline $\delta^{15}N$ signal, an average rock bass $\delta^{15}N$ trophic position of 3.87 (Cabana and Rasmussen 1996; Vander Zanden et al. 1997) was substituted in the above trophic position equation and then solved for baseline $\delta^{15}N$. This method provided a baseline, primary consumer $\delta^{15}N$ estimate of 6.1‰ for the Detroit River. With this baseline estimate, rock bass and bluegill $\delta^{15}N$ trophic position estimates averaged 3.6 and 3.3, respectively, in good agreement with $\delta^{15}N$ trophic positions derived from the literature for these species (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). The resulting predicted $\delta^{15}N$ signatures are in good agreement with previously reported values for these prey categories collected from the Detroit River – Lake Erie corridor (Table 2).

In generating the mixed prey $\delta^{15}N$ signature estimates for age-class diets, the proportions of prey category in the diet were corrected for using the respective coefficients of variation for each prey category by the factor ($\%\text{diet}_n \times 11 - \text{CV}$). This was completed to account for within age class prey category variability as observed during gut contents analysis in the prediction of mixed prey dietary $\delta^{15}N$ signatures (Table 3). Dietary $\delta^{15}N$ ER values for rock bass and bluegills were then calculated as the difference between the average $\delta^{15}N$ signatures and the predicted dietary $\delta^{15}N$ value for each year class (Table 3). Year-class $\delta^{15}N$ enrichment rates were also calculated by solving eq. 3 for ER. Specific growth rates determined for each year class of rock bass and bluegill were used to estimate enrichment of $\delta^{15}N$ resulting from growth (g). The metabolic turnover rate (m) of 0.0018 day^{-1} calculated by Hesslein et al. (1993) was allometrically scaled in a similar manner as described for the chemical elimination rate constants (k_2) in the PCB accumulation model to generate the modeled ER values (Table 3).

Statistical methods

Statistical analyses were completed using SYSTAT version 8.0 for Windows (Wilkinson 1998) with a criterion for significance of $p < 0.05$ used in all cases. All data were tested for normality using normal probability plots. PCB results exhibited nonnormal distributions and heteroscedasticity and therefore were subsequently $\log_{10}$-transformed. Stable nitrogen isotope results were found to be normally distributed and no data transformation was necessary. For all analyses of variance (ANOVA), a Scheffé's postsignificance test was used because of differences in sample sizes between groups in the analyses (Zar 1984). Relationships between $\delta^{15}N$ and ΣPCB concentrations (lipid weight) in rock bass

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Table 3. Summarized biological, stable isotope, and pollutant data for rock bass (*Ambloplites rupestris*) and bluegill (*Lepomis macrochirus*) age classes.

Species	Age (years)	N	Average total length (cm)	Average mass (g)	Specific growth rates		Average $\delta^{15}N$ (‰)	Predicted dietary $\delta^{15}N$ (‰)	Predicted $\delta^{15}N$ enrichment rates (‰)		Average ΣPCB (μg·g lipid^{-1})
					(%·day^{-1})	(%·year^{-1})			Dietary	Modeled	
Rock bass	YOY	5[a]	4.7 (0.3)	1.6 (0.3)	0.88	321	10.9 (0.2)	8.7	2.2	2.2	2.0 (0.2)
	1	5	8.4 (0.1)	9.1 (0.2)	0.48	175	11.3 (0.2)	8.2	3.1	3.1	2.7 (0.3)
	2	5	11.4 (0.2)	28.8 (1.5)	0.32	117	11.5 (0.5)	8.1	3.4	3.4	2.6 (1.3)
	4	5	16.4 (0.5)	97.9 (9.8)	0.17	62	11.8 (0.1)	8.8	3.1	3.0	17.6 (6.2)
	6	3	23.2 (0.3)	211.1 (0.3)	0.11	40	12.9 (0.1)	9.2	3.7	3.7	13.4 (5.9)
	7	2	23.9 (0.2)	248.2 (0.3)	0.04	15	12.8 (0.2)	9.1	3.7	3.7	21.6 (17.0)
Bluegills	YOY	5[a]	6.2 (0.1)	4.5 (0.3)	0.93	339	10.3 (0.1)	7.5	2.8	2.8	0.8 (0.1)
	1	5	10.8 (0.3)	25.2 (2.7)	0.49	179	10.6 (0.2)	7.4	3.1	3.2	0.9 (0.2)
	3	2	14.5 (0.2)	71.5 (9.5)	0.14	51	10.6 (0.8)	7.4	3.1	3.3	5.0 (1.5)
	4	3	17.2 (0.2)	113.9 (5.4)	0.12	44	12.1 (0.3)	7.8	4.2	4.3	4.6 (0.2)

Note: Where average results are reported, values represent the arithmetic means (±1 standard error). Specific growth rates were calculated using eq. 7. Predicted dietary $\delta^{15}N$ results were generated using the dietary mixing model outlined in eq. 9. Modeled $\delta^{15}N$ enrichment rates were calculated by solving eq. 3 for ER (see Materials and methods). YOY, young-of-the-year.

[a]Pooled samples consisting of at least three individuals per sample (see Materials and methods).

and bluegills were analysed by linear regression. Linear and nonlinear regression modules in SYSTAT were used to determine the best-fit regression models describing the relationship between $\delta^{15}N$ enrichment rate and body mass for rock bass and bluegills. Regression analyses were not corrected for outliers.

To address potential statistical uncertainty, the statistical power ($1 - \beta$) of all regressions and ANOVAs were determined using power analysis of the correlation coefficients and ANOVAs using the methods outlined by Zar (1984). These analyses indicated the potential of type II statistical error (β) associated with the $\delta^{15}N$ vs. ΣPCB regressions to be 27% ($1 - \beta = 0.73$) and 16% ($1 - \beta = 0.84$) for rock bass and bluegills, respectively. Among the regression analyses completed, the highest probability of committing a type II statistical error ($\beta = 0.41$) was associated with the positive relationship described between bluegill body mass and $\delta^{15}N$. For ANOVAs, a maximum probability of type II error was associated with the comparison of ΣPCB concentrations between rock bass age classes where a β value of 0.012 was calculated. For all other multiple-comparison tests, calculated β values were lower than that estimated for the rock bass age-class ΣPCB ANOVA.

Results

A total of 211 rock bass and 33 bluegills ranging in mass from approximately 1 to 246 g (4–24 cm) and 2 to 142 g (5–18 cm), respectively, were collected. Including YOY, a total of six rock bass and four bluegill age classes were identified. Gut contents of rock bass indicated general omnivory for YOY and 1-year-olds, with small cyprinids constituting ~24% of the diet by age 1 (Table 4). By age 2 ($\bar{x}$ = 28.8 g), cyprinids had become the dominant diet item in rock bass gut contents, constituting approximately 67% of prey items in fish ≥2 years of age, and were the only prey observed in age-4 fish gut tracts. At 6 years of age ($\bar{x}$ = 211.1 g), large (~75 mm) crayfish constituted approximately 33% of prey items, with the rest made up of cyprinid forage fish for individuals ≥6 years of age.

No major shifts in diet were observed in bluegills, with amphipods and trichopterans combining to total at least 50% of the prey items for YOY ($\bar{x}$ = 6.2 g) and age-1 fish ($\bar{x}$ = 25.2 g) and trichopterans accounting for approximately 31% of the diet by age 4 (Table 4). Gastropods were identified in the gut tracts of all bluegills and were the sole prey item for 3-year-old fish. Zebra mussels were observed only in the diet of 1-year-old fish. No evidence of prey size selectivity was observed with increasing bluegill body size or age.

ΣPCB concentrations ranged from 1 to 34 μg·g^{-1} (lipid weight) for individual rock bass and from 0.4 to 6 μg·g^{-1} for bluegills (Table 3). Analysis of variance and a Scheffé's postsignificance test demonstrated significantly higher ΣPCB concentrations in rock bass 4 years of age ($\bar{x}$ = 97.9 g) and older than those reported for younger, smaller individuals ($p = 0.001$). For bluegills, ΣPCBs in fish 3 years of age ($\bar{x}$ = 71.5 g) and older were significantly higher ($p < 0.001$) than those reported for the two younger age classes. In both species, no significant differences between ΣPCBs were observed among age classes of fish with average weights ≤~30 g. Highest average ΣPCB concentrations of 21.6 μg·g^{-1} were

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Table 4. Mean dietary data for rock bass (*Ambloplites rupestris*) and bluegill (*Lepomis macrochirus*) age classes.

	Age classes						
Prey category	YOY	1	2	3	4	6	7
Rock bass							
Arachnida	36.8 (1.0)	8.4 (3.0)	—		—	—	—
Cladocera	4.5 (3.2)	—	—		—	—	—
Copepoda	2.7 (4.9)	—	—		—	—	—
Amphipoda	5.9 (2.7)	13.2 (1.9)	3.0 (3.3)		—	—	—
Trichoptera	44.0 (0.9)	11.9 (2.4)	9.1 (3.3)		—	—	—
Diptera	0.6 (8.7)	19.7 (1.8)	3.0 (3.3)		—	—	—
Cyprinidae	—	23.5 (1.7)	75.8 (0.6)		100.0	66.7 (0.3)	66.7 (0.5)
Decapoda	—	0.8 (4.1)	—		—	33.3 (0.6)	33.3 (1.0)
Detritus–other	5.6 (2.9)	22.5 (1.6)	22.4 (3.3)		—	—	—
Bluegills							
Amphipoda	28.4 (1.4)	37.6 (1.4)		—	—		
Trichoptera	45.0 (0.9)	22.3 (2.3)		—	31.0 (1.7)		
Gastropoda	16.1 (2.4)	6.7 (7.8)		100.0	69.0 (0.8)		
Pelycypoda	—	6.7 (7.8)		—	—		
Detritus–other	10.5 (3.7)	26.7 (1.9)		—	—		

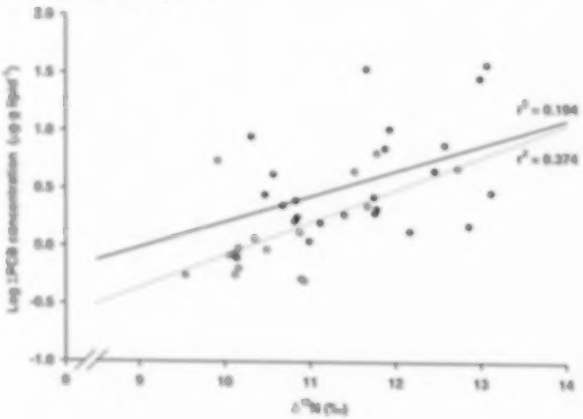
Note: Values represent the average percent of total prey items enumerated in individual fish gut tracts (±1 standard error). YOY, young-of-the-year.

measured in the largest rock bass size class ($\bar{x}$ = 248.2 g). Coefficients of determination describing the relationships between $\delta^{15}N$ and log-transformed, lipid weight corrected ΣPCB concentrations for rock bass and bluegills were found to be 0.374 and 0.194, respectively (Fig. 1).

A comparison of three specific PCB congener concentrations ranging in log K_{ow} from 5.7 (PCB 28) to 6.9 (PCB 153) demonstrated biomagnification for contaminants of log $K_{ow} \geq 5.8$ as a function of increasing mass in both species (Figs. 2, 3). PCB congeners 28, 52, and 153 did not exhibit any significant increases in concentration by ~30 g for rock bass or bluegills, with PCB 28 concentrations remaining consistent regardless of body mass for either species. However, by ~70 and 100 g in mass for rock bass and bluegills, respectively, ANOVA indicated that concentrations of the more hydrophobic PCB congeners 52 (log K_{ow} = 5.8) and 153 (log K_{ow} = 6.9) were significantly higher than those reported for PCB 28 ($p < 0.001$).

The PCB bioaccumulation model described in eq. 6 accurately predicted the contaminant accumulation patterns observed in the field data for congeners 28, 52, and 153 (Figs. 2*a*, 3*a*). The estimated accumulation profile for PCB 28 (log K_{ow} = 5.7) did not predict any increase in concentration of this chemical with increased body size for either species. For PCBs 52 and 153, however, congener concentrations were predicted to begin increasing by 25–30 g in size and, in rock bass, were observed to reach an inflection point by ~100 g in size after which no further increases in chemical accumulation were predicted. In bluegills, congeners 52 and 153 were predicted to increase with bluegill body mass >25 g; however, modeled concentrations for PCB 153 were below the observed values measured in larger (>70 g) bluegills and were predicted to continue increasing with larger mass. For PCB 52, the predicted concentration trend accurately reflected the concentrations reported in larger individuals. In general, these bioaccumulation profiles are in agreement with the field data in which significant increases in ΣPCBs were observed in fish >70 g relative to those measured in smaller individuals. Further, the significant increases in concentration for the more hydrophobic (log $K_{ow} \geq 5.8$) PCB congeners occurred in both species when ≤60% of the total body mass was replaced on annual basis (Table 3). For younger fish <30 g, however, high specific growth rates resulted in body mass at least doubling in 1 year of growth with no significant increases in PCB concentrations observed.

Fig. 1. Relationship between log-transformed, lipid-normalized Σ polychlorinated biphenyl (PCB) concentrations and $\delta^{15}N$ in rock bass (*Ambloplites rupestris*) and bluegills (*Lepomis macrochirus*). Individual rock bass and bluegill sunfish are represented by the open and solid circles, respectively, with the solid and dotted lines representing the respective least squares regression lines for the two species.



To better understand PCB accumulation in the smallest individuals (≤1 year old), chemical concentrations for these individuals were contrasted with steady state corrected concentrations calculated for 20 PCB congeners measured in freshwater mussels (*Elliptio complanata*) deployed at the study site (Fig. 4; O'Rourke 2004). PCB concentrations in

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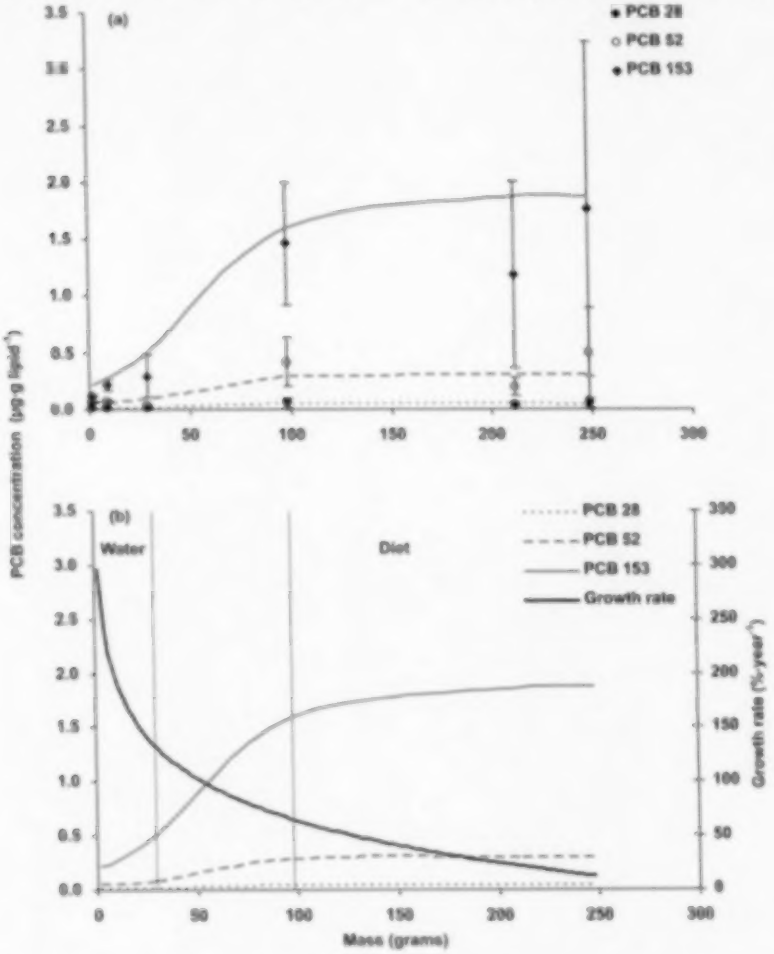
Fig. 2. (*a*) Relationships between polychlorinated biphenyl (PCB; congeners 28, 52, and 153) concentrations and rock bass (*Ambloplites rupestris*) body mass. Symbols represent the arithmetic means of each congener concentration with error bars indicating ±1 standard error. Dotted, dashed, and solid lines represent the predicted PCB accumulation profiles for PCB congeners 28, 52, and 153, respectively, with increased rock bass body mass. (*b*) Relationship between rock bass annual growth rates (%·year^{-1}) and predicted PCB congener accumulation profiles. Area between vertical lines indicates body mass range where contaminant exposure transitions from water-based bioaccumulation kinetics (bioconcentration) to accumulation dominated by dietary exposure (biomagnification). Logarithmic growth curve is represented by the thick, solid line. In both panels, PCB congener accumulation profiles were estimated using the model outlined in eq. 6.



the smallest rock bass ($\bar{x}$ = 1.6 g) were not significantly different (Student's *t* test, $p = 0.216$) from those reported for the mussel biomonitors; however, by an average size of ~9 g, rock bass PCB concentrations were significantly higher than mussel levels ($p = 0.019$). For bluegills, all PCB concentrations closely reflected those reported in the mussel biomonitors, with the smallest size class ($\bar{x}$ = 4.5 g) having significantly lower ($p < 0.001$) contaminant levels than those for mussels. By an average size of ~25 g, no significant differences were observed between bluegill and mussel PCB concentrations. On average, PCB concentrations in the smallest (YOY) rock bass and bluegills were, respectively, 1.4 to 0.5 times mussel concentrations. By the next year of growth, average PCB concentrations in rock bass were double those for mussels, with bluegills having concentrations approximately 70% of the mussel levels. Although PCB concentrations in YOY and 1-year-old rock bass were slightly more enriched for congeners of log $K_{ow} < \sim 7.0$ relative to mussel levels, this relationship was not significant ($r^2 = 0.045$, $p = 0.367$). For bluegills averaging ≤25 g, no significant relationship between log K_{ow} and relative PCB concentrations was observed ($r^2 = 0.001$, $p = 0.925$).

BMFs estimated for PCB congeners 28, 52, and 153 were correlated with body size for both species, with the most substantial increases observed for PCB 153 in both species (Table 1). BMFs for PCB 153 in bluegills ranged from 7.6 for the smallest individuals to a high of 30.5 for a 3-year-old fish averaging 72 g. For this congener in rock bass, BMFs ranged from 9.3 to 14.7 among all sizes, with the highest value estimated for individuals ~100 g average mass. Although BMFs for PCB congeners 28 and 52 increased with body size, this pattern was not of the same magnitude as that

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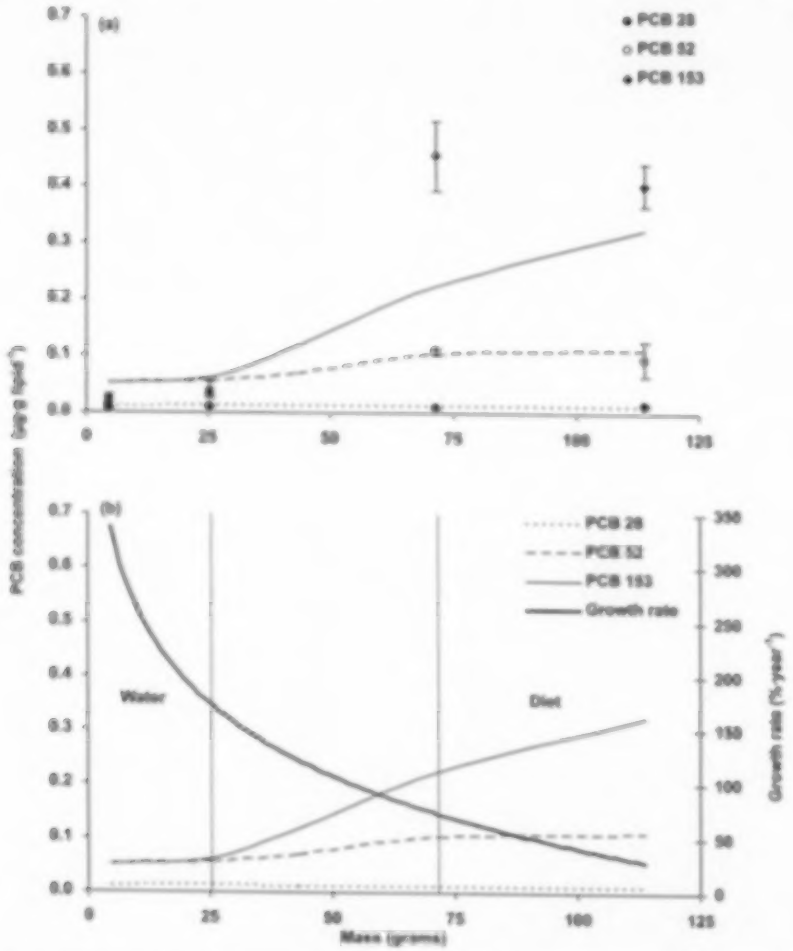
Fig. 3. (*a*) Relationships between polychlorinated biphenyl (PCB; congeners 28, 52, and 153) concentrations and bluegill (*Lepomis macrochirus*) body mass. Symbols represent the arithmetic means of each congener concentration with error bars indicating ±1 standard error. Dotted, dashed, and solid lines represent the predicted PCB accumulation profiles for PCB congeners 28, 52, and 153, respectively, with increased bluegill body mass. (*b*) Relationship between bluegill annual growth rates (%·year^{-1}) and predicted PCB congener accumulation profiles. Area between vertical lines indicates body mass range where contaminant exposure transitions from water-based bioaccumulation kinetics (bioconcentration) to accumulation dominated by dietary exposure (biomagnification). Logarithmic growth curve is represented by the thick, solid line. In both panels, PCB congener accumulation profiles were estimated using the model outlined in eq. 6.



observed for PCB 153. From the smallest to largest bluegill sizes, BMFs increased 117%, 257%, and 145% for PCBs 28, 52, and 153, respectively. For rock bass, however, BMFs for these three congeners exhibited an average increase of 41% from the smallest to largest individuals. Between both species and among all sizes, average BMFs calculated for these three congeners corresponded well with the values of 2.1, 2.9, and 16 reported for PCBs 28, 52, and 153, respectively, by Fisk et al. (1998).

Rock bass δ^{15}N values ranged from 10.9‰ to 12.9‰ across the size range of fish collected, with the upper range measured in the second-largest size class ($\bar{x}$ = 211.1 g; Table 3). δ^{15}N values were positively correlated with both mass and age in both species; however, these relationships were significant for rock bass only (Fig. 5*a*; p = 0.001). For bluegills, average δ^{15}N results ranged from 10.3‰ in the smallest ($\bar{x}$ = 4.5 g) fish to 12.1‰ for the largest ($\bar{x}$ = 113.9 g) individuals. δ^{15}N signatures in these large bluegills were also significantly enriched relative to the two smallest size classes (p = 0.020). A Student's t test indicated that rock bass δ^{15}N results were significantly higher than the bluegill isotope values (p = 0.001).

Dietary δ^{15}N values generated by the mixing model calculations predicted an increase in dietary nitrogen signature from 8.7‰ to a high of 9.2‰ as rock bass grew in average size from 1.6 to 211.1 g (Table 3). A slight decrease to 9.1‰ was predicted for the dietary δ^{15}N signature in the largest size class ($\bar{x}$ = 248.2 g) of rock bass, primarily due to increased variability in the proportion of cyprinids observed in the diet. The increased proportion of detritus in age-1 rock

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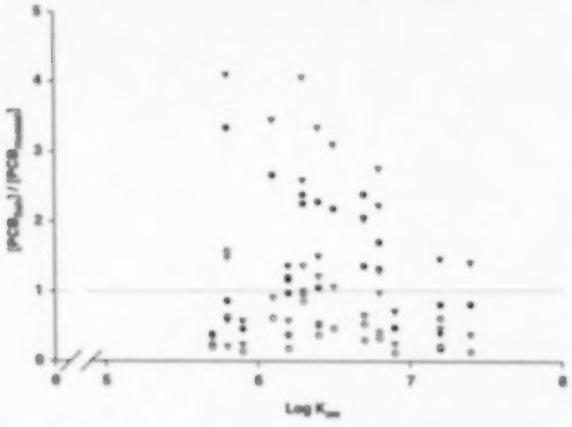
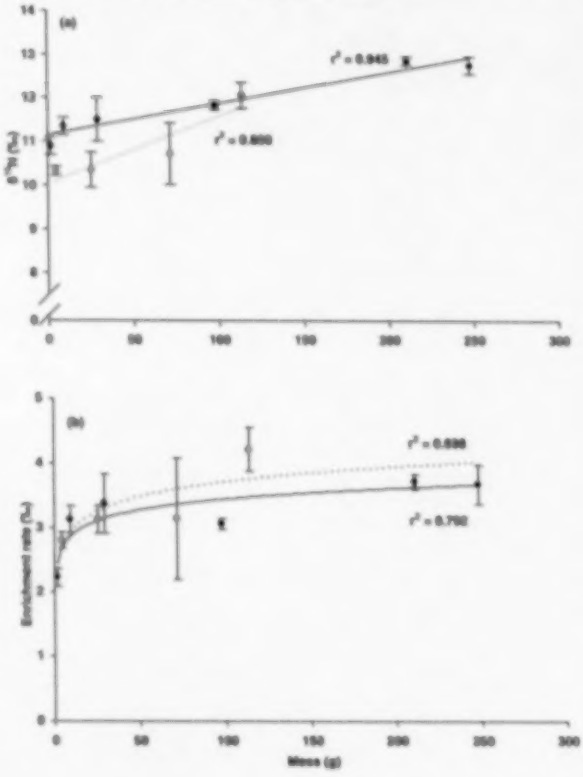
Fig. 4. Relationship between relative polychlorinated biphenyl (PCB) congener concentrations in young-of-the-year (YOY) and 1-year-old fish and congener hydrophobicity (log K_{ow}). Average lipid weight PCB concentrations for rock bass (*Ambloplites rupestris*) and bluegill (*Lepomis macrochirus*) are expressed relative to steady state corrected PCB concentrations previously reported for freshwater mussels (*Elliptio complanata*) deployed in the Detroit River (O'Rourke 2004). Individual rock bass and bluegill sunfish are represented by the solid and open symbols, respectively, with YOY and 1-year-old fish represented by circles and inverted triangles, respectively. Dotted line represents 1:1 ratio for steady state corrected mussel PCB concentrations.



bass guts combined with fewer water mites resulted in a predicted mixed-prey $\delta^{15}N$ of 8.2‰, slightly lower than that predicted for the smallest size class diet even though cyprinids were approximately one-quarter of the diet for age-1 fish. Predicted bluegill diet $\delta^{15}N$ values exhibited a marginal increase from 7.5‰ to 7.8‰ among the size range of fish, with no changes in dietary $\delta^{15}N$ calculated for individuals averaging 25.2–71.5 g in size.

The estimates of $\delta^{15}N$ ER were similar whether calculated from the difference between measured $\delta^{15}N$ signatures in fish and the predicted dietary $\delta^{15}N$ signatures or using the model outlined in eq. 3 (Table 3). The largest difference between ER predictions was that for age-3 bluegills, where the dietary calculation indicated an ER of 3.1‰ compared with 3.3‰ estimated by the kinetic model for this age class. Both methods also demonstrated that ER increased with body size, with the relationship observed between ER and mass for both species best described by log-linear functions (Fig. 5*b*). Using the dietary method, average ER values for rock bass and bluegills were 3.0‰ and 3.2‰, respectively. For rock bass, the average ER values predicted for the two largest size classes were identical at 3.7‰. Significant differences were observed between size-class ER values in both species using the dietary estimates ($p = 0.036$). For rock bass, this was primarily due to the difference in ER between the smallest ($\bar{x} = 1.6$ g) and second-largest ($\bar{x} = 211.1$ g) size classes. In bluegills, ER values for the largest size class were significantly higher ($p = 0.003$) than those observed for all other sizes. ER values were also negatively correlated with specific growth rates in both rock bass ($r^2 = 0.434$) and bluegills ($r^2 = 0.410$).

Fig. 5. Relationships between (*a*) stable nitrogen isotope signatures and (*b*) stable nitrogen enrichment rate over the diet and rock bass (*Ambloplites rupestris*) and bluegill (*Lepomis macrochirus*) mass. Individual rock bass and bluegill sunfish are represented by solid and open symbols, respectively. The solid and dotted lines represent the least squares (*a*) linear and (*b*) nonlinear regression lines for rock bass and bluegills, respectively. Enrichment rates are those calculated as the difference between predicted dietary $\delta^{15}N$ signatures and age-class average $\delta^{15}N$ values. Error bars indicate ±1 standard error.



Discussion

The rock bass and bluegill diet analyses yielded prey types and proportions similar to those documented in the literature for these species (Mittelbach 1981; Rabeni 1992; Vander Zanden et al. 1997). The more enriched rock bass $\delta^{15}N$ signatures relative to those of bluegills confirm the predatory nature of this species and its higher trophic position in this food web. The ontogenetic diet shift to piscivory was first observed in 1-year-old rock bass averaging ~9 g in size. Bluegills diets, however, continued to be dominated by small invertebrates, notably trichopterans and gastropods, regardless of size. Invertebrate diets typically have a higher proportion of indigestible material (chitin) compared with piscivory (Stewart et al. 1983), and consumption rates must increase accordingly to meet daily energetic requirements (Pazzia et al. 2002). Consequently, foraging costs are much higher for predators feeding on small invertebrates, resulting

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in lower growth efficiencies and growth rates (Pazzia et al. 2002). For bluegills, no evidence of size selectivity was observed in the diet, and growth efficiency is expected to be negatively correlated with predator–prey size ratios and decrease faster in predators feeding on smaller prey (Kerr 1971*a*, 1971*b*; Pazzia et al. 2002). By 4 years of age, rock bass diets were dominated by cyprinid prey, resulting in a growth rate 40% higher than that estimated for bluegills of the same age feeding exclusively on invertebrates. These observations suggest that although bluegills may benefit from the ease of capture of smaller, sessile prey, such costs may be minimal and are offset by the increased time and energy spent foraging to obtain a given growth rate.

The resultant PCB concentrations measured in the smallest (YOY) individuals were similar to those reported for freshwater mussel (*Elliptio complanata*) deployed at the study site (O'Rourke 2004). Freshwater mussels are excellent monitors of chemical residues in aquatic systems because of their ability to accumulate contaminants primarily from water (Gewurtz et al. 2003; O'Rourke et al. 2004), with chemical uptake regulated by bioconcentration kinetics as described by eq. 5. ΣPCBs in the smallest rock bass and bluegills averaged 1.4 and 0.5 times those of mussels, respectively, with concentrations increasing to double and 70% of those in mussels by the first full year of growth. Additionally, no chemical hydrophobicity trends were evident for these sizes of fish, and only minor enrichment of PCB congeners of log $K_{ow} < 7.0$ was observed for these sizes of rock bass. Both of these patterns suggest that these small fish have either achieved steady state or reached equilibrium with respect to PCB concentrations in water. Olsson et al. (2000) concluded that contaminant concentrations in small (<100 g) Eurasian perch (*Perca fluviatilis*) had reached steady-state levels as no significant increases in concentrations or hydrophobicity effects were evident. Both the observed data and PCB accumulation model predictions did not demonstrate any significant increases in PCB concentrations until bluegills and rock bass attained body masses of 72 g and 98 g, respectively. The lack of significant chemical accumulation observed in smaller fish has been attributed to a combination of physiological characteristics including rapid growth rates, large gill surface area to body mass ratios, and high chemical elimination relative to uptake (Sijm et al. 1992, 1995; Olsson et al. 2000). The high growth rates calculated for individuals ≤ ~30 g in size indicates that growth dilution is an important factor regulating chemical accumulation in these fish. However, the model (eq. 4) used to predict PCB bioaccumulation consistently overpredicted concentrations for small fish. This is likely a result of underestimates in elimination and growth dilution occurring in YOY fish. These results conform to the general prediction of life-cycle bioaccumulation models which indicate that chemical accumulation from water (bioconcentration) dominates uptake in early life stage fish as a result of rapid growth dilution and relatively high rates of gill elimination (Sijm et al. 1992).

The consideration of POPs as bioenergetics tracers is only tenable when uptake from food dominates the exposure pathway. For chemicals of log $K_{ow} > 5.5$, dietary uptake is the primary source, with biomagnification mechanisms dictating the extent of bioaccumulation (Thomann et al. 1992). BMFs for PCB 153 (log $K_{ow} = 6.9$) in both species were observed to increase with body size. By ~25 g in size, specific growth rates for both species were sufficiently high to result in at least a doubling of body mass annually, and the difference between BMFs for PCB 153 across small sizes were negligible. However, at ~100 g in size, the PCB 153 BMF for bluegills was estimated at 18.6, and the specific growth rate had slowed (<50% of the body mass was replaced annually). For rock bass of similar size, a higher annual growth rate resulted in a larger proportion of the body mass gained, with a lower BMF of 14.7 estimated for PCB 153. From eq. 4, BMF describes the ratio of chemical uptake from food to losses through elimination, as well as growth. Chemical uptake from the diet, however, is the product of feeding rate and assimilation efficiency of the chemical from the food (Morrison et al. 1997). Thus, for individuals of ~100 g in mass, the higher PCB 153 BMF reported for bluegills indicates that this species must consume more food energy and thus accumulate more PCBs to achieve the same growth as rock bass of similar size. Ignoring potential species differences in chemical assimilation and k_2 values, the differences in PCB 153 BMFs suggest growth conversion efficiencies to be at least 26% higher in rock bass compared with bluegills of similar age and size. This conclusion is supported by the lower growth efficiencies associated with insectivorous diets (Pazzia et al. 2002). Further, regardless of size, bluegills continued to forage on small prey, a characteristic expected to correlate to faster decreases in growth efficiency than size-selective feeding (Kerr 1971*a*, 1971*b*). Such lower growth efficiency may have explained the tendency of the PCB accumulation model to underpredict PCB congener concentrations in the two largest bluegill age classes. These data suggest that growth conversion efficiencies and the bioenergetics associated with the different foraging strategies and resultant growth rates play important roles in regulating the degree of chemical bioaccumulation observed in larger size classes of fish.

The degree of stable nitrogen isotope ER estimated for small (YOY) bluegills (2.2‰) and rock bass (2.8‰) differs substantially from that calculated for all other sizes of fish in this study. Average ER for all rock bass and bluegills ≥1 year old were 3.4‰ and 3.5‰, respectively, in good agreement with the widely held average of trophic level enrichment for $\delta^{15}N$ of 3.4‰ reported by Minagawa and Wada (1984) and the range exhibited by a variety of aquatic species (Vander Zanden and Rasmussen 2001). For small, rapidly growing fish, high specific growth rates are expected to result in isotopic signatures more closely associated with dietary steady state than those of slowly growing fish (Hesslein et al. 1993). Such trends were not apparent in the present study; instead, the relationships between ER and mass for both species were best described by log-linear functions that were not expected to stabilize until the second year of growth. Such differences in isotopic enrichment provide important information on feeding and metabolic rates that are lost in the assumption of a constant $\delta^{15}N$ trophic level enrichment factor (Olive et al. 2003). These results emphasize the need for further experimentation to understand size- and growth-related differences in isotopic enrichment rates (Olive et al. 2003).

Significant correlations between $\delta^{15}N$ and chemical concentrations have been demonstrated in freshwater food webs

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(Kidd et al. 1995; Kiriluk et al. 1995), but these relationships typically fail to hold when examined within species (Kiriluk et al. 1995; Kidd et al. 1998; Berglund et al. 2001). Correlations were observed between $\delta^{15}N$ and ΣPCB concentrations for both species; however, these relationships were weak. Chemical accumulation in small fish is limited by high growth and elimination rates and also water-to-fish bioconcentration kinetics (Gobas and Mackay 1987; Sijm et al. 1992; Olsson et al. 2000). Subsequently, marginal increases in chemical accumulation are expected until growth reaches the mass at which transition in chemical accumulation becomes dominated by uptake from the diet (Clark et al. 1990; Sijm et al. 1992, 1995). Therefore, the rapid changes expected in young, fast-growing predator $\delta^{15}N$ signatures (Hesslein et al. 1993; Vander Zanden et al. 1998) will not be combined with concurrent increases in chemical accumulation until growth reaches the body mass at which dietary uptake predominates chemical exposure and elimination across the respiratory surface is minimal.

For larger individuals, gape-limited prey consumption is less restricted and a wider size spectrum of organisms becomes potential prey (Persson et al. 1996), leading to omnivory (feeding at more than one trophic level), opportunistic feeding, and trophic variability that obscure relationships between trophic position and body size (Vander Zanden et al. 2000). Consequently, $\delta^{15}N$ in larger fish represents a long-term integration of potential changes in dietary $\delta^{15}N$ signature (Hesslein et al. 1993). Chemical accumulation will be primarily through dietary uptake, thereby leading to significant increases in chemical concentrations as dictated by the bioenergetics of growth, metabolism, and foraging behaviour in larger individuals. By using primarily older, mature individuals, especially for top predators (Kiriluk et al. 1995; Kidd et al. 1998), and composite samples (Kidd et al. 1995), the relationships between $\delta^{15}N$ and chemical concentrations for entire food webs mask such influences of species bioenergetics. Through investigation of intraspecific relationships between $\delta^{15}N$ and contaminant concentrations, the importance of age, growth, and size on such correlations become clearer.

Much of the kinetics associated with chemical accumulation has been well defined and quantified (i.e., Morrison et al. 1997). For $\delta^{15}N$, however, less is known of the mechanisms regulating assimilation, fractionation, and elimination and there is a substantial need for research in this area (Gannes et al. 1997; Olive et al. 2003). The poor relationship observed between $\delta^{15}N$ and lipid-corrected PCB concentrations in this study and in other species (Kiriluk et al. 1995; Olsson et al. 2000; Berglund et al. 2001) provides evidence that these ecological markers track processes regarding food web dynamics or metabolic and physiological parameters. For $\delta^{15}N$, food web trophic structure and specific trophic interactions such as predator–prey relationships can be depicted with this ecological descriptor (Vander Zanden and Rasmussen 1996). Persistent organic pollutant concentrations, such as PCBs, however, represent a species life history of energy acquisition, assimilation, and growth efficiency and thus are appropriately interpreted as bioenergetic tracers.

This research identified some of the difficulties associated with the application and interpretation of stable isotopes and persistent organic pollutants as ecological tracers for rapidly growing YOY and age-1 size classes. The differences in chemical accumulation between small, rapidly growing fish and larger, more slowly growing individuals are a consequence of changes in bioaccumulation mechanisms that occur in response to shifts in body mass and the relative importance of growth to chemical dilution and elimination kinetics. Similar shifts in isotope enrichment ratios, as observed in this study, may reflect differences between the fractionation mechanisms predominating under rapid growth vs. maintenance growth conditions. To characterize changes in chemical and isotope kinetic parameters in different species and over life history changes, further information will be essential to increase the interpretive value of stable isotopes and chemicals as ecological tracers in aquatic systems.

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Integrating marine protected areas with catch regulation

Ray Hilborn, Fiorenza Micheli, and Giulio A. De Leo

Abstract: Previous models of marine protected areas (MPAs) have generally assumed that there were no existing regulations on catch and have frequently shown that MPAs, by themselves, can be used to maintain both sustainable fish stocks and sustainable harvests. We explore the impact of implementing an MPA in a spatially structured model of a single-species fish stock that is regulated by total allowable catch (TAC). We find that when a stock is managed at maximum sustainable yield, or is overfished, implementation of an MPA will require a reduction in TAC to avoid increased fishing pressure on the stock outside the MPA. In both cases, catches will be lower as a result of overlaying an MPA on existing fisheries management. Only when the stock is so overfished that it is headed towards extinction does an MPA not lead to lower catches. In a TAC-regulated fishery, even if the stock is overfished, MPA implementation may not improve overall stock abundance or increase harvest unless catch is simultaneously reduced in the areas outside the MPA. Models that consider differential adult and larval dispersal need to be explored to see if these results are found with the more complex biology of a two-stage model.

Résumé : Les modèles antérieurs de zones de protection marine (« MPA ») présupposent généralement qu'il n'y a pas de règlements actuels sur les captures et ils ont souvent démontré que les MPA, par elles-mêmes, peuvent servir à maintenir tant des stocks soutenables de poisson que des récoltes soutenables. Nous examinons l'impact de l'établissement d'une MPA dans un modèle structuré en fonction de l'espace d'un stock monospécifique de poissons qui est contrôlé par la capture totale permise (« TAC »). Lorsqu'un stock est géré à un rendement maximum soutenable ou qu'il est surexploité, l'établissement d'une MPA exige la réduction de TAC pour éviter une pression accrue de la pêche sur le stock à l'extérieur de la MPA. Dans les deux cas, les captures vont diminuer puisque la MPA se surajoute à la gestion actuelle de la pêche. C'est seulement lorsque le stock est tellement surexploité qu'il risque l'extinction que la MPA ne cause pas de réduction des captures. Dans une pêche commerciale réglementée par TAC, même lorsque le stock est surexploité, l'établissement d'une MPA peut ne pas améliorer l'abondance globale du stock, ni augmenter la récolte, à moins que la capture ne soit simultanément réduite dans les zones extérieures à la MPA. Il faudra explorer les modèles qui tiennent compte de la dispersion différente des adultes et des larves afin de voir si les mêmes résultats sont obtenus d'un modèle à deux niveaux avec une biologie plus complexe.

[Traduit par la Rédaction]

Introduction

In recent years considerable attention has been paid to the implementation of networks of marine protected areas (MPAs) as a method to protect marine biodiversity and help manage fisheries (Allison et al. 1998). Although less than 1% of coastal marine environments are currently protected in MPAs (Roberts and Hawkins 2000), numbers of newly established MPAs have been increasing rapidly, and the implementation of more extensive reserve networks is underway in several nations (e.g., the Great Barrier Reef (Australia), the Channel Islands (California, USA), and the Bahamas; Airamé et al. 2003).

MPA establishment is frequently associated with increased abundance, biomass, and sizes of focal species, increased total abundance, biomass, and diversity of all species, and changes in the structure of species assemblages (Palumbi 2001; Halpern and Warner 2002; Micheli et al. 2004). In addition to enhancing populations and assemblages within the protected area, MPA establishment can increase catch-per-unit-effort (CPUE) in adjacent areas through export of juveniles and adults (Yamasaki and Kawahara 1990; Russ and Alcala 1996; Roberts et al. 2001). However, empirical evidence of increased fishery catches following reserve establishment is still controversial. In particular, increased catches may not be sufficient to compensate for the decreased extent of the fishing grounds to produce greater total yields, at least in the short term (e.g., McClanahan and Mangi 2000). Because of the difficulty of documenting MPA effects on fishery yields, questions about the effective-

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ness of MPAs for fisheries management have been addressed largely through modeling (reviewed by Guenette et al. 1998; Botsford et al. 2003; Gerber et al. 2003).

Models of MPAs have shown that effects on yield depend on dispersal in the larval, juvenile, and adult stages, size and configuration of reserves, and status of the fishery. Over the past decade, models of MPAs have produced three generalizations about effects on fishery yields. First, MPA establishment is expected to increase yields when fishing effort cannot be controlled and populations would otherwise be overfished, but it is unlikely to improve yields of lightly fished fisheries (Holland and Brazee 1996; Sladek-Nowlis and Roberts 1999; Gerber et al. 2003). Second, for MPAs to be effective, rates of adult fish movement cannot be too high. As adult movement rates increase, larger MPAs are needed to achieve gains (Polacheck 1990). Species with low movement rates receive the greatest benefits from MPAs in terms of increased reproductive potential, but these benefits rarely move out of the reserve to contribute to the fishery. Thus, fishery gains are expected to be greatest for species with intermediate rates of movement (DeMartini 1993; Botsford et al. 2003). Finally, MPAs reduce variability in catches in the face of stochastic events such as recruitment failures (Sumaila 1998; Sladek-Nowlis and Roberts 1999) and make fisheries less sensitive to uncertainty in fishing mortalities (Lauck et al. 1998; Mangel 2000).

Much of the traditional analysis focuses on how MPAs compare with conventional fishery management using size limits, effort control, or regulation of total catch (TAC). Models addressing this question indicate that the effect of reserves on yields is similar to increasing the age of first capture or to reducing effort (Botsford et al. 2003). In their classic analysis, Beverton and Holt (1957) examined the effects of using reserves as a management tool by assuming that after reserve establishment, fishing effort would become concentrated in a smaller area and that movement between unfished and fished areas is in proportion to abundances in the source area. As the extent of the unfished area increases, the shape of the relationship between yield per recruit and fishing mortality changes in a similar way to what results from assuming greater age limits (Beverton and Holt 1957; Guenette et al. 1998). As noted above, both large unfished areas and high age limits maintain high yields when the population is overfished. Several models have indicated that the establishment of MPAs is equivalent to a reduction in fishing mortality rate in a nonspatial management context (Quinn et al. 1993; Holland and Brazee 1996; Hastings and Botsford 1999). In particular, Hastings and Botsford (1999) showed that for species with sedentary adults, dispersal through a larval pool, and postdispersal density dependence, the selection of optimal MPA size is mathematically identical to the determination of optimal fishing mortality rate.

In most developed countries where large-scale MPA networks are being proposed, existing fisheries management systems are in place, which include gear, effort, and often TAC limitation. Thus, in practice, MPAs will not be established as alternatives to existing fisheries management, but as additions to it. Accordingly, models have either removed fishing effort as a function of reserve size or have increased fishing mortality outside MPAs (e.g., Beverton and Holt 1957; Holland and Brazee 1996). Spatial analyses of fishermen redistribution among patchy resources indicate that fishermen behavior needs to be integrated within models (e.g., Sanchirico and Wilen 1999; Stefansson and Rosenberg 2005). Stefansson and Rosenberg (2005) explored regulatory structures that mixed effort controls, total catch controls, and closed areas and concluded that a mix of these three approaches provided the best combination of economic yield and buffering against uncertainty. Rodwell and Roberts (2004) explored the consequences of reserves under constant harvest rate TACs but assumed that the TAC depended only on the population outside the reserve, thus there was implicitly a TAC reduction at the time of TAC implementation. Thus MPA establishment also implied TAC reduction. To our knowledge, no study has examined the effects of establishing MPAs within an existing management system when the spatial dynamics of target populations, fishing fleet, and regulated catches are included.

The purpose of this paper is to explore the consequences of imposing a system of MPAs on top of an existing fisheries management system that limits catches by setting an annual TAC. We specifically test the hypotheses that establishment of MPAs will increase both population abundance and fisheries yields. To do this we use the spatially explicit model described below.

Materials and methods

Our model assumes a linear array of 100 areas such as might occur along a coastline. The underlying assumptions are logistic growth in each area, with movement each year distributing individuals to other areas as a decreasing function of distance to those areas. A list of symbols used in the equations is provided in Table 1.

The basic model equations for each area before movement are logistic growth with harvesting:

$$(1) \qquad N'_{i,t+1} = \left(N_{i,t} + N_{i,t} r \left(1 - \frac{N_{i,t}}{k} \right) - u_{i,t} N_{i,t} \right)$$

The fish are then moved according to a movement probability matrix:

$$(2) \qquad N_{i,t+1} = \sum_{j=1}^{n} N'_{j,t+1} p_{j,i}$$

The movement matrix is calculated by assuming that the movement probability has a normal shape centered on the area of origin:

$$(3) \qquad p'_{j,i} = \exp\left(-\frac{(i-j)^2}{2m^2} \right)$$

which is normalized to sum to one for each donor area:

$$(4) \qquad p_{j,i} = \frac{p'_{j,i}}{\sum_i p'_{j,i}}$$

This model is highly simplistic in that there is no spatial heterogeneity and no stochasticity in the dispersal process.

We assume that the population initially is at some fraction of its carrying capacity:

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Table 1. List of symbols.

Symbol	Definition
A	Number of areas in the reserve
B	Total number of boats in the entire model
$B'_{i,t}$	Intermediate variable that is the relative number of boats in an area
$B_{i,t}$	Number of boats in area i at time t
c	Parameter that determines how boats aggregate in areas of the most abundance
d	Initial population size as a fraction of carrying capacity
I	Intercept of the catch vs. stock size relationship
K	Carrying capacity in each area
m	Movement distance parameter
$\tilde{N}$	Maximum abundance of fish outside the reserve
$N'_{i,t}$	Number of individuals in area i at time t before movement
$N_{i,t}$	Number of individuals in area i at time t after movement
$P_{i,j}$	Probability of an individual moving from area i to area j
q	Fraction of the stock in an area harvested by each boat
r	Intrinsic rate of increase in each area
s	Slope of the catch vs. stock size relationship
TAC_t	Total allowable catch over all areas in year t
$u_{i,t}$	Fraction harvested in area i at time t
z	Proportional reduction in fishing effort in all areas required to make total catch equal to the TAC

(5) $$N_{i,1} = dK_i$$

Reserve implementation and harvest

A total of a areas are set aside in a reserve, in the middle of the total linear array of areas. The year of first establishment of the MPA is adjustable.

Boats are allocated to areas based on the abundance of fish in the areas outside the reserve, no vessels fish inside the reserve. Let $\tilde{N}$ be the maximum abundance outside the marine reserve in any given year; the following two-step process allocates boats along the fishery (subscripts for time have been dropped for simplification):

(6) $$\begin{cases} B'_i = \exp\left[-c\left(1-\dfrac{N_i}{\tilde{N}}\right)\right] & \text{if area } i \text{ is not in a reserve} \\ B'_i = 0 & \text{if area } i \text{ is in a reserve} \end{cases}$$

$$B_i = B\frac{B'_i}{\sum_i B'_i}$$

These equations cause boats to concentrate in places of highest fish abundance. Therefore as the value of c increases, the concentration of boats also increases.

The fraction harvested in each area is determined by the number of boats, the efficiency of boats (q), and a scaling factor when regulations reduce the allowable catch (z).

(7) $$u_{i,t} = B_{i,t} q z$$

Regulations

Each year, the fishing vessels are allowed to operate until the overall catch equals the annual limit, namely the TAC. The TAC can be set through a flexible rule (Hilborn and Walters 1992) that can represent a constant harvest rate, a fixed escapement, a constant catch, and many intermediate policies, that is

(8) $$\mathrm{TAC}_t = \left[I + s\sum_A N_{i,t}\right]$$

where I is the intercept and s is the slope of a relationship between TAC and total number of fish summed over all areas inside and outside the MPA. If I is set to 0, then s represents a constant harvest rate. For instance, TAC can be computed by setting the harvesting rate to the value s that would guarantee the maximum sustainable yield (MSY) in an homogeneous population with the same demographic parameters (reproductive rate and carrying capacity) but no spatial dynamics of the larvae and (or) fishes and of the fleet and no restriction to the fishing areas.

If the catch that would occur without regulation is less than the TAC, then the regulations have no effect. If the catch that would occur without regulation is greater than the TAC, then the catch in each area is reduced proportionally so that the total catch is equal to the TAC by adjusting the scaling factor z.

(9) $$z = \frac{\mathrm{TAC}_t}{\sum_i qB_{i,t}N_{i,t}}$$

As a consequence, the total effective harvest in any given year is computed as follows:

$$\text{Total harvest}_t = \sum_i u_{i,t}N_{i,t}$$

$$= \begin{cases} \sum_i qB_{i,t}N_{i,t} & \text{if } \sum_i qB_{i,t}N_{i,t} < \mathrm{TAC}_t \\ \mathrm{TAC}_t & \text{if } \sum_i qB_{i,t}N_{i,t} \geq \mathrm{TAC}_t \end{cases}$$

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Fig. 1. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 1, where stock was headed towards extinction until a marine protected area was implemented.

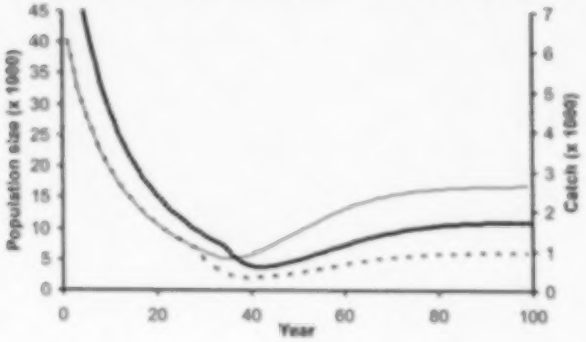
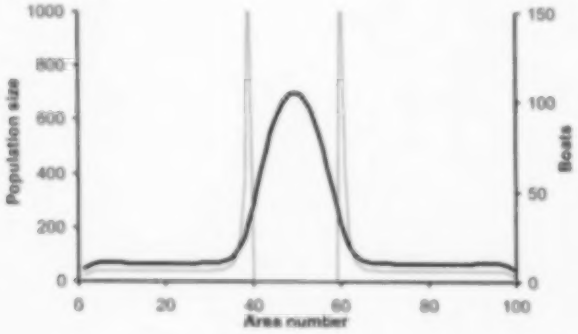


Fig. 2. Distribution of boats and fish after 100 years in scenario 1. Thick line is the abundance of fish, the thin line is the number of boats.



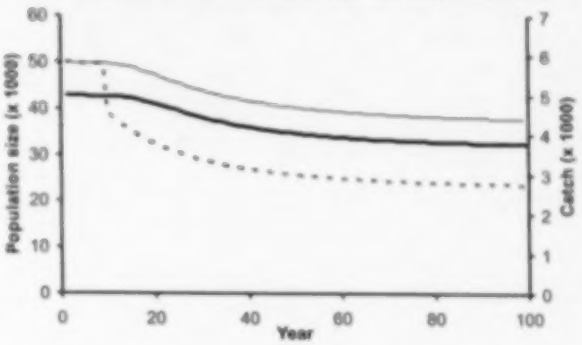
Further assumptions

In all scenarios, we have assumed that one MPA of size 20 is implemented in the middle of the 100-unit area, corresponding to 20% of the area in MPAs. The stock always has an intrinsic rate of increase of 0.2 and a carrying capacity in each area of 1000. Under these assumptions, it follows that harvest rate that guarantees the MSY, namely s_{MSY}, is equal to 10%, whereas the corresponding population size at equilibrium and catch over the coastline are 50 000 and 5000 fishes, respectively. Harvesting rates equal to, or exceeding, 20% would lead to population extinction.

In these simulations, the total number of fishing boats B is 1000 and q is 0.3, which means that if evenly spread across 100 areas, the exploitation rate in each area would be 30%, which is sufficient to drive the population in each area to extinction. As a consequence, in the absence of a TAC regulation or an MPA, the population would be driven to extinction.

The fleet aggregation parameter c has been set to 5 so that fishing effort is mainly clustered along the edges of reserves where fish density is higher. The fish movement rate m is set to 3, which allows significant spillover from a reserve. To test the sensitivity of our results to values for c and m, we ran further simulations using values that range from 1 to 5 for c and from 1 to 10 for m. A value of $c = 1$ means that the fleet is reasonably uniformly distributed outside the reserve. Increasing values of c provide for increasing concentration of fishing effort at the locations of highest fish abundance. A value of $m = 1$ means that the population is almost sedentary, with little spillover outside the reserve. A value of $m = 10$ means that the stock is highly mobile and there is little effect on the reserve.

Fig. 3. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 2, where stock was at maximum sustainable yield before marine protected area implementation.



Results

To illustrate the basic functioning of the model, scenario 1 assumes that the stock begins at $K/2$, but the fishery is poorly regulated and the overall harvest rate is 0.2, so it is headed towards extinction (Fig. 1). In year 30, the MPA is implemented, allowing the stock to rebuild inside the MPA and providing spillover to areas outside the MPA, which in turn leads to a rebuilding of total abundance and catch. The distribution of boats and fish in year 100 of this scenario are illustrated (Fig. 2) with the boats accumulating on the edge of the MPA, and the fish abundance high in the center of the MPA but declining towards its edges. This is a classic illustration of how an MPA can provide increases in yield in an overfished system and prevent population extinction. However, total population size and harvest from this system (50 000 and 5000, respectively) is far less than at MSY. In scenario 2 (Fig. 3), all parameters are the same except that the stock is harvested at s_{MSY} (10% per year), holding the stock at the MSY from before implementation of the MPA. When the marine reserve is implemented, management rules still require the annual TAC to be computed as 10% of the overall stock, namely the sum of individuals inside and outside the MPA. The result of the MPA is to cause both the stock size and the catch to decline slightly. In fact, before MPA implementation, the exploitation rate is exactly optimal for MSY management. After the MPA, the fleet can operate only outside the MPA but keeps fishing until the TAC is removed: as a consequence, the harvest rate outside the MPA is higher than s_{MSY}, and thus the stock declines.

In scenario 3 (Fig. 4), all parameters are the same again except that before MPA implementation, the stock is just at one-tenth of its carrying capacity K, i.e., quite overfished, and the TAC is computed by setting the harvest rate s (eq. 8) at 15% per year, a level that will allow the stock to rebuild

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Table 2. Comparison of results for a range of movement rates and fleet aggregation parameters when the exploitation rate is 10% and provides maximum sustainable yield.

	Fleet aggregation parameter (c)				
Movement rate (m)	1	2	3	4	5
1	0.08, 0.37	0.07, 0.36	0.08, 0.36	0.11, 0.38	0.17, 0.41
2	0.17, 0.34	0.18, 0.32	0.22, 0.34	0.27, 0.37	0.32, 0.40
3	0.55, 0.54	0.67, 0.66	0.72, 0.72	0.75, 0.75	0.77, 0.77
4	0.77, 0.77	0.82, 0.82	0.85, 0.85	0.87, 0.87	0.88, 0.88
5	0.85, 0.85	0.89, 0.89	0.90, 0.90	0.92, 0.92	0.92, 0.92
6	0.90, 0.90	0.92, 0.92	0.93, 0.93	0.94, 0.94	0.95, 0.95
7	0.93, 0.93	0.94, 0.94	0.95, 0.95	0.96, 0.96	0.96, 0.96
8	0.94, 0.94	0.95, 0.95	0.96, 0.96	0.96, 0.96	0.97, 0.97
9	0.95, 0.95	0.96, 0.96	0.97, 0.97	0.97, 0.97	0.97, 0.97
10	0.96, 0.96	0.97, 0.97	0.97, 0.97	0.97, 0.97	0.98, 0.98

Note: The first number in each cell is the ratio of catch with a reserve to catch without a reserve. The second number is the ratio of total population with a reserve to total population without a reserve.

Fig. 4. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 3, where stock was rebuilding from overexploitation before marine protected area implementation.

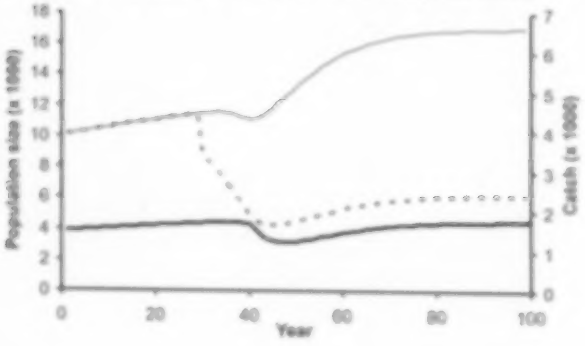
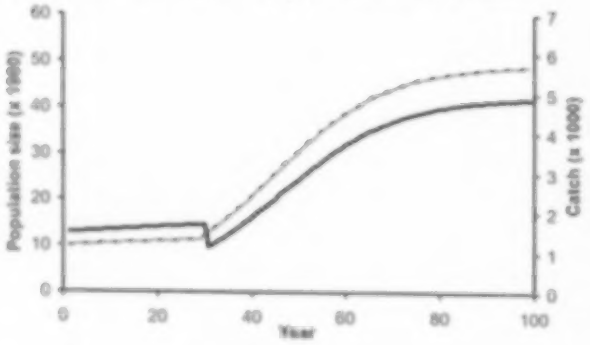


Fig. 5. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 4, where stock was rebuilding from overexploitation before year 30, when harvest rate is reduced to 10%. No reserve is implemented in this scenario.



but still remain overfished. The simulations show that when the MPA is implemented, both catch and stock abundance first decline, then the catch recovers to its previous level and the total stock increases significantly. At the end of 100 years, the catch is the same as it would have been without the MPA, but total abundance is higher. However, both catch and stock remain well below the level that they would have achieved by setting annual TAC at MSY (that is, $s = s_{MSY} = 10\%$) with no MPA (scenario 4). Again, when MPA is implemented, a significant portion of the total population cannot be harvested inside the MPA, so the TAC (computed as 15% of the overall stock inside and outside the MPA) can be harvested only outside the MPA; as a consequence, the actual exploitation rate outside the MPA increases substantially above 15%, and thus the population outside the reserve is strongly depleted. The increase in population abundance within the MPA in not able to compensate for the drop in abundance outside the marine reserve.

Scenario 4 (Fig. 5) is identical to scenario 3 except that no MPA is implemented. Instead, the harvest rate s to compute TAC is reduced to its MSY level, namely at 10%, in year 30. Both catch and biomass rebuild faster without an MPA and reach higher equilibrium levels than observed in scenario 3.

The effect of the implementation of an MPA is shown for a range of m and c values in a TAC-regulated fishery that is already at its MSY equilibrium ($s = s_{MSY} = 10\%$) (Table 2). We can see that when movement rates are high ($m > 6$), there is very little impact of the reserve, and catch and population size are almost the same with or without the reserve. However, when movement is low ($m < 3$), the impact of the reserve is remarkable. The fishes inside the reserve provide little spillover outside the reserve, while overall TAC is allocated outside the reserve, and as a consequence, stocks outside the reserve are heavily overfished. The catch is greatly diminished and the total population size is lower than without a reserve because the only fish left are found inside the reserve.

Although the impact of movement is very dramatic, the impact of the fleet aggregation parameter c is less so. However, when the fish movement rate is low, catch is considerably higher at higher fleet concentration values, which is when the fleet aggregates at the edge of the reserve and concentrates on the fish that do spillover.

The results of an MPA implemented in a fishery with an annual TAC of 15% of the overall stock, which leads to overexploitation but not extinction of the fish population, are reported in Table 3 as the relative performance of an MPA in

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Table 3. Comparison of results for a range of movement rates and fleet aggregation parameters when the exploitation rate is 15% and the population will be overfished.

	Fleet aggregation parameter (c)				
Movement rate (m)	1	2	3	4	5
1	0.20, 1.39	0.18, 1.35	0.19, 1.34	0.26, 1.41	0.42, 1.56
2	0.41, 1.27	0.39, 1.19	0.40, 1.18	0.52, 1.29	0.71, 1.48
3	0.59, 1.12	0.55, 1.00	0.58, 0.99	0.72, 1.12	0.88, 1.29
4	0.66, 0.90	0.58, 0.73	0.59, 0.71	0.69, 0.81	0.81, 0.94
5	0.56, 0.61	0.49, 0.48	0.59, 0.59	0.66, 0.66	0.71, 0.70
6	0.61, 0.60	0.72, 0.72	0.79, 0.79	0.83, 0.82	0.85, 0.85
7	0.76, 0.75	0.83, 0.83	0.87, 0.87	0.89, 0.89	0.91, 0.91
8	0.84, 0.84	0.89, 0.89	0.91, 0.91	0.93, 0.93	0.94, 0.93
9	0.89, 0.89	0.92, 0.92	0.93, 0.93	0.94, 0.94	0.95, 0.95
10	0.91, 0.91	0.94, 0.93	0.95, 0.95	0.96, 0.95	0.96, 0.96

Note: The first number in each cell is the ratio of catch with a reserve to catch without a reserve. The second number is the ratio of total population with a reserve to total population without a reserve.

Table 4. Comparison of results for a range of movement rates and fleet aggregation parameters when the exploitation rate is 20% and the population would be driven to extinction without a reserve.

	Fleet aggregation parameter (c)				
Movement rate (m)	1	2	3	4	5
1	12.3, 121	11.5, 117	11.5, 117	14.0, 120	25.3, 136
2	25.5, 110	24.1, 103	24.2, 102	29.7, 110	43.2, 128
3	36.1, 97.3	33.5, 86.2	33.9, 84.2	41.1, 94.8	52.4, 110
4	37.3, 74.2	30.9, 57.3	29.7, 53.0	34.3, 59.8	40.9, 69.9
5	23.7, 38.5	13.9, 20.5	11.4, 16.0	12.3, 17.3	14.3, 20.2
6	8.92, 12.0	3.79, 4.54	2.82, 3.24	2.88, 3.30	3.24, 3.75
7	2.91, 3.36	1.18, 1.22	0.96, 0.96	0.97, 0.97	0.97, 0.97
8	1.14, 1.17	0.97, 0.97	0.98, 0.98	0.98, 0.98	0.98, 0.98
9	0.97, 0.97	0.98, 0.98	0.98, 0.98	0.98, 0.98	0.99, 0.99
10	0.98, 0.98	0.98, 0.98	0.99, 0.99	0.99, 0.99	0.99, 0.99

Note: The first number in each cell is the ratio of catch with a reserve to catch without a reserve. The second number is the ratio of total population with a reserve to total population without a reserve.

an overharvested TAC fishery with respect to a fishery harvested at its MSY ($s = s_{MSY}$). Although implementation of an MPA might be beneficial to fish abundance (but not to catch) for lower values of m in the case of moderate overfishing, simulations show that the establishment of an MPA is never as effective as regulating the fishery by setting the annual TAC to its MSY (namely, by reducing s to s_{MSY}). We know this because at MSY (s = 10%), yield is higher than when $s = 15\%$, and the implementation of MPAs with $s = 15\%$ never provides increased yields. In fact, by implementing an MPA in an overfished stock ($s = 15\%$), the equilibrium harvest is about 40% of that achieved at MSY and the equilibrium population size is about 20% of that at MSY. As in Table 2, adding a reserve has little impact when movement rates are high and both catch and population size are about the same. When movement rates are low, again the reserve leads to considerably reduced catch but now leads to higher population sizes. With low movement rates, the populations inside the reserve build to near-virgin condition, while there are few fish outside the reserve. From a population abundance perspective, reserves provide major benefits, but there are no benefits in terms of fisheries yields.

The results for a harvest rate $s = 20\%$, which leads to extinction in the long term, are shown in Table 4. In the 100 years of simulation, the population is reduced to very low numbers in the absence of a reserve. As long as movement rates are low enough (<7), both catch and population size are better with a reserve in place. This is consistent with what we observed in Fig. 1. Thus, reserves result in both population and fisheries benefits when stocks are heavily overfished.

Discussion

This simple model illustrates that the consequences of MPA implementation on both stock abundance and yield will depend on the regulations used to limit catch and that MPA implementation may even have negative consequences on abundance and catch of a TAC-regulated fishery at its MSY if harvesting strategies are not simultaneously modified and vessels allowed to remove all the TAC (computed on the overall stock) outside the MPA. Under these conditions, MPA implementation can slow down rather than increase stock-rebuilding rates (scenarios 3 and 4), and even when the stock is overexploited, we found no catch benefits from MPA establishment unless overexploitation is so intense that stocks are headed towards extinction in the absence of protection though MPA. Thus, MPA implementation may

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not increase fish yields if the fishery is already regulated unless the fishery is heavily overexploited. We have shown results for only a single value for the rate of increase, but because the dimensions of movement rate and rate of increase are scalable, the results should be very general.

This counterintuitive result is easily understood in the spatial context. The allowable harvest set by the regulatory agency on the basis of the overall stock (inside and outside the MPA) will be removed from fewer spatial areas after the MPA is implemented, leading to overexploitation outside the MPA that is not compensated for by the export of individuals from inside the MPA. For the movement rate to be low enough to provide rebuilding inside the MPA, the effect of shifting all of the allowable harvest to 80% of the total area is to provide for more intense exploitation in those areas. Although it might seem reasonable to recalculate the TAC based only on the fish outside the reserve, this will cause a decline in catch, and the joint effect of an MPA and TAC-reduction policy would need to be compared with catch reduction alone (scenario 4). In general, the results are more pronounced when fish movement is low. As movement rates are increased, the MPA has less impact overall. This is consistent with all previous MPA models. We explored a range of the fleet concentration parameter (c), and although it did affect how much of the effort was concentrated at the edge of the reserve, it did not affect the temporal pattern of total catch and stock size.

We also performed further simulations to explore the effects of implementing several smaller reserves rather than just a large one so as to increase the ratio of edge to interior of reserve. As expected, this appears to be identical to increasing the movement rate. For instance, 20% of the area divided into three reserves with the same movement rates provided almost no "reserve effect" and abundance did not increase significantly inside the reserves. Previous models of MPA impacts have not considered existing catch regulations, yet such regulations are the rule rather than the exception in Canadian and US fisheries, where the harvesting effort (as here measured by the number of fishing boats) is so high that it would rapidly deplete the stock if a limit to the allowable catch were not set. We have not considered stochastic dynamics or formalized the uncertainty in stock assessment to which MPAs should provide a buffer. Scenario 3 does have the management regulation at a level that would be considered overfishing in the US (15% harvest rate), which can be thought of as a form of management error. We recognize that the large uncertainties associated with the assessment of stock sizes, unwillingness of managers to reduce catches when stocks are overfished, and lack of compliance with regulations in many places in the world render the management of fisheries with traditional catch and effort control ineffective. Thus our analysis and results are intended to demonstrate that when catch limits are indeed effective, MPA implementation will need to be coordinated with such catch limits. In contrast, scenario 1 shows that when catch limits are ineffective and stocks are headed towards extinction, MPAs are effective in maintaining some biomass and catches. Similarly, MPAs are expected to reduce variability in catches in the face of stochastic variation in recruitment (Sumaila 1998; Sladek-Nowlis and Roberts 1999) and uncertainty in fishing mortalities (Lauck et al. 1998; Mangel 2000), which we did not include in this model.

This analysis (as in almost all previous models of MPAs) is a single-species evaluation and like most current fisheries management ignores the ecological and evolutionary consequences of harvesting marine populations in coastal ecosystems. MPAs and other spatial approaches to management are promising tools for addressing uncertainty and long-term maintenance of populations and ecosystems. Nevertheless, our model results suggest that the effectiveness of MPAs as a fisheries management tool is likely to be influenced by other regulations in place. If significant areas are placed in MPAs, existing TACs will likely need to be reduced to prevent declines in abundance of some species following MPA implementation and concentration of fishing effort outside reserves. In fact, to be effective, TACs need to be computed only on the fraction of the population that is actually harvestable and not on the overall stock inside and outside the MPA. We thus suggest that any future analysis of MPA implementation on fisheries abundance and yield needs to explicitly consider the catch regulatory structure that is in place when the MPAs are introduced.

Important research priorities include determining how including real system complexities into this simple model may influence the conclusions and developing general rules for how to integrate MPAs with existing regulations. We made no attempt to select model parameters to show specific results and thus cannot claim that any particular quantitative results are general. However, we found no combinations of parameters that had a significant MPA effect on abundance inside the reserve that did not show that catches outside the reserve would need to be reduced at the time of MPA implementation. The key message from this initial model is that MPA implementation and traditional TAC regulation may interact in unexpected ways.

A next step in model analysis is to consider models in which larvae disperse more broadly than adults. In addition to adult and juvenile movement, increased reproductive output from older, larger individuals inside MPAs and larval dispersal to adjacent fished areas are means by which MPAs are expected to increase fishery yields (Bohnsack 1992; Palumbi 2001). Including larval dispersal and possible effects of the changed age and size structures on fecundity and reproductive outputs are critical for increasing the biological realism of future models.

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Modelling population viability in fragmented environments: contribution to the conservation of an endangered percid (*Zingel asper*)

Jacques Labonne and Philippe Gaudin

Abstract: *Zingel asper* is an endemic percid of the Rhône catchment. The demography and habitat use of this endangered benthic species have been studied in previous works. The species exhibits natural low densities and clumped distribution related to habitat distribution. Based on these results, the authors build a stochastic equations network model, integrating spatial structure at intrapopulation level and vague density dependence. Calculation of density, growth rates, and local extinction rates globally match the field results. The numerical sensitivity analysis on extinction probabilities shows that adult and juvenile survival rates and spawning success (due to random events) are the key parameters of intrapatch dynamics. Low negative variations in these parameters increase extinction probabilities. The number of available connected patches and the dispersal rate drive the population persistence at the interpatch scale. Population extinction probability over 100 years is at least 0.4 for dispersal rate below 0.2, or when the number of connected patches is below 15. These results enlighten the role of dispersal in nonmigratory fish populations and should be useful in assessing the impact of riverine habitat fragmentation through river-damming and habitat loss.

Résumé : *Zingel asper* est un percidé endémique du bassin versant du Rhône. La démographie et l'utilisation de l'habitat chez cette espèce ont été étudiés dans des travaux antérieurs. L'espèce présente des densités naturellement faibles, ainsi qu'une distribution agrégative liée à la distribution des habitats. A partir des données existantes, les auteurs construisent un réseau d'équations stochastiques, qui intègre la structure spatiale à l'échelle même de la population, ainsi qu'un mécanisme de densité-dépendance vague. Les densités, taux de croissance démographiques ainsi que les probabilités d'extinction locale obtenus par le modèle correspondent globalement aux données de terrain. Une analyse numérique de sensibilité montre que les taux de survie des adultes et des jeunes et le succès de la fraie (en fonction d'évènements aléatoires) sont les paramètres clefs de la dynamique intra-patch. A l'échelle inter-patch, le nombre de patch connecté et le taux de dispersion conditionnent la persistance de la population. Pour un taux de dispersion égal à 0,2, et un nombre de patch connecté inférieur à 15, la probabilité d'extinction sur 100 ans est supérieure à 0,4. Ces résultats illustrent le rôle de la dispersion chez les populations de poissons non migrateurs et devraient permettre d'estimer l'impact de la fragmentation de l'habitat fluvial causé par la construction de barrages et la perte d'habitats.

Introduction

Conservation of aquatic resources has been recognized as one of the crucial goals for biodiversity management, as water use for human activities is often in conflict with species persistence. Freshwater fishes are especially threatened (Meffe and Caroll 1994), but their conservation has gathered the attention of a growing number of biologists (Collares-Pereira et al. 2002). It is now well accepted that small population size and declining population numbers are often considered as the main concerns of conservation biology (Simberloff 1988; Ballou et al. 1995; Foose et al. 1995). The concept of population viability analysis (PVA) focuses on the extinction risk associated with these two cases. This concept has been extended to the case of metapopulations (Hanski 1999) to account for dispersal and spatial structure of populations (Grimm et al. 2004). The fragmented aspect of theoretical metapopulations seems adapted to the problem of habitat loss and fragmentation on large scales (Gilpin 1995; Schlosser and Angermeier 1995; Tilman and Kareiva 1997). However, the fragmentation at the intrapopulation level is also likely to affect persistence. In the context of conservation biology, one can expect the role of dispersal to be dramatically important. Indeed, in the original metapopulation

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theory, initial properties of the system imply a large number of connected populations (Hanski 1999). In the case of endangered species, the biologist often deals with small numbers of isolated habitat patches at a small scale (i.e., inside a population). As a consequence, special attention should be devoted to the modelling of spatial structure at the intrapopulation level.

Many PVA are based on life cycles. Some biological or behavioural functions, such as dispersal in nonmigratory species, can sometimes be underestimated or simply forgotten. This point is especially true in freshwater fishes, where it is often difficult to record movement rates and modalities and where the restricted movement paradigm has long prevailed (Gerking 1959). Recent studies tend to show that dispersal at small, medium, and high ranges could be common in riverine fish (Fausch and Young 1995; Lucas and Baras 2001; Belanger and Rodriguez 2002). At the same time, the spatial structure of habitat is particular and very constraining: there is only one possible path to move from one given place to another (Fagan et al. 2002).

We applied the PVA approach to a population of an endangered percid, *Zingel asper*. This endemic benthic fish has been included in the International Union for Conservation of Nature and Natural Resources (IUCN) Red List since 1996 and is also listed in the Habitats Directive of the European Commission (Annexes II and IV) and in the Bern Convention (Annex II). The European Commission supported a LIFE–NATURE Program with "Reserves Naturelles de France" in 1998 to gather biological information and to develop conservation strategies for the species. Here, we propose a PVA accounting for environmental variability, demographic stochasticity, and carrying capacity (Strong 1985; Botsford 1995). We model a heterogeneous habitat distribution at the intrapopulation level. Our first goal was to determine if a model based on estimated parameters could replicate field observations and data (Labonne and Gaudin 2005). We then addressed two questions with this model. (*i*) What are the main factors influencing the extinction probability of the system? (*ii*) In the metapopulation theory, low dispersal rates allow the persistence of the system (Levins 1970; Hanski 1999). In our case, where local patch densities can be small and the number of patches is reduced, some high rates were detected in the field. Are such rates essential for the viability of our population?

Materials and methods

Study species

Zingel asper is an endemic percid inhabiting the Rhône catchment in southern France. This benthic predator seldom exceeds 20 cm long, with many adults measuring between 10 and 17 cm (Cavalli et al. 2003). Two viable populations remain: one in the River Durance and the other in the River Beaume. The latter was monitored from 1998 to 2002. Spawning usually occurs in March. Maturity is reached after 1 year, but little is known about spawning behavior or early life stages. Habitat selection in the wild has been studied (Labonne et al. 2003), and selection for hydraulic microhabitats has been demonstrated. These habitat preferences explain the patchy distribution observed in the field, where fish clearly aggregate in particular morphodynamic sequences (that we called patches) along the river: they tend to strongly select run and riffle habitats for both growth and spawning activities, whereas pools, channels, and rapids are clearly avoided. Field data revealed low natural densities (about 20–40 per hectare; J. Labonne and P. Gaudin, unpublished data) in these patches and even lower densities between patches. A study of movement at small scales (i.e., intrapatch) showed that fish were very mobile and exhibited various movement patterns conditional on the season (growth, spawning) and sex (Danancher et al. 2004). At larger scales, demographic analyses estimated low adult survival rates and a random recruitment success (Labonne and Gaudin 2005). Estimates of population annual growth rates, λ, varied between 0.8 and 1.2. Scale analysis showed that most adult mature fish were 2 or 3 years old, with a maximum age of 5 years (D. Danancher, Laboratoire d'Ecologie des Hydrosystèmes Fluviaux, Université Lyon 1, F-69622 Villeurbanne, France (Delphine.Danancher@univ-lyon1.fr), unpublished data). Labonne and Gaudin (2005) also hypothesized a high dispersal between patches (5%–25% of patch abundance) but for short distances (i.e., 2 km, which corresponds to two patches in this river). No event of long-range dispersal occurred during the monitoring of the Beaume population, nor is it reported in the literature. However, dispersal would be higher than expected for this benthic species. Such a result was not frequently reported in sedentary riverine fish (Gerking 1959; Northcote 1998; but see Gowan and Fausch 1996).

Model parameterization

The essence of the Leslie's matrix model is to formalise a discrete network of i equations, under precise conditions, to take advantage of the analytical properties of the matrix (Leslie 1945; Caswell 2001). In our case, demographic stochasticity and the density-dependent evolution of some demographic parameters limited the application of a classic Leslie matrix approach. We thus transformed the matrix model into a branching process, which can be seen as a network of equations with each equation describing the relation between the ith age class at time t and other age classes at time $t - 1$ (Fujiwara and Caswell 2001). The time step was annual. The structure of the equations is given in Appendix A.

Demographic structure

The life cycle was divided in two stages: juvenile stage (with abundance J) and adult–reproductive stage (with abundance A; Fig. 1) with a prebreeding census. Fish enter the first stage at about 1 year after birth and do not spawn during the first stage until almost 2 years old. They then join the second stage, becoming adult and being able to spawn. The adult stage was not divided into age subclasses because there was no evidence of relationship between age and survival in adults in our data.

Adult and juvenile survival rate

Capture–mark–release data indicate that annual adult ($s3$) and juvenile ($s2$) survival rates are around 0.5 (Labonne and Gaudin 2005). We used this value in our model, integrating also its temporal variations: the mean adult survival rate was 0.5 and its standard deviation was 0.02, which implies a 10% variation, congruent with the variation observed in our data. Field results showed that no more than 120 fish (older

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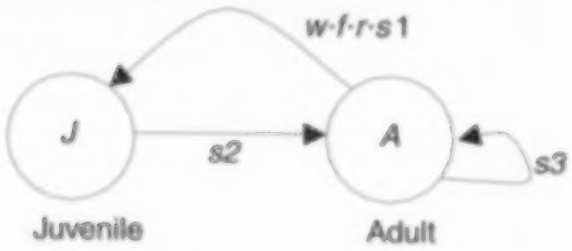

Fig. 1. Life cycle design into a patch. *J* and *A* are the density of each stage, *s*3 is the adult survival rate, *w* is the spawning success, *f* is the fecundity, *r* is the sex ratio, *s*1 is the larva survival rate, and *s*2 is the juvenile survival rate.

than 6 months) could inhabit the same patch. Even if stochastic variations can limit density and produce extinction, they do not prevent diverging trajectories, which remains an unrealistic option and may highly bias the persistence time (Middleton et al. 1995). We decided to integrate an upper limit in each patch (carrying capacity, *C*), corresponding to 120 adult individuals in the initial model, so that the local adult density per patch generated by the model could not exceed *C*.

Larval survival rate

In many fish species, the larval survival rate cannot be easily estimated through field analysis. In *Z. asper*, alevins (0–2 months) were never found in the natural environment. However, recruitment and population growth rates have been estimated (see Labonne and Gaudin 2005). It was possible to deduce the mean larval survival rate necessary to make the model match the observed annual population growth rate in the field ($\lambda \approx 0.8$–1.2, without density limitation). This approach allowed the computation of a mean value of 0.005 (95% confidence interval (CI): 0.00275, 0.00775). Thus, in our model, the larval survival rate (*s*1) was represented by the corresponding log-normal probability distribution of mean = 0.005 and standard deviation (SD) = 0.001. This estimate integrates the hatching success rate and the survival rate during the first year.

Fecundity rate

Fecundity is linked to body size in fish, which is highly variable regardless of the age class. This parameter was not estimated in a previous study, and it was not possible to sacrifice any individuals to improve our estimates. Therefore our estimation of fecundity relied on egg counts from eight females (four from the Musée d'Histoire Naturelle de Lyon (Lyon, France), two from the collections of the Université de Grenoble (Grenoble, France), and two from the field). From the regression of egg numbers (N_{egg}) on fish total length (L_t) ($N_{egg} = 35.174L_t - 3283.8$), we estimated a mean number of eggs per female based on fish size distribution in our population. Depending on sampling dates and stations, fish size distribution varied significantly, giving values of mean fecundity from 1117 to 1366 (i.e., number of eggs per female). To simplify the results, a log-normal distribution ($\mu = 1200$, $\sigma = 300$) was used to compute the number of eggs (*f*) to mimic the effect of size distribution in the population. The sex-ratio estimation in the field was realised during two sampling campaigns during the spawning season (when sex could be determined), and it was not different from 1. Thus, we considered an equilibrated sex ratio in the model.

Spawning success

The spawning success was highly variable in the field, and total failures of recruitment were observed in several stations (Labonne and Gaudin 2005). Field data from 1997 to 2004 showed that substantial recruitment was exhibited in only 3 years and recruitment was almost nonexistent in 5 years (D. Dunancher, Laboratoire d'Ecologie des Hydrosystèmes Fluviaux, Université Lyon 1, F-69622 Villeurbanne, France (Delphine.Dunancher@univ-lyon1.fr), unpublished data). To take this fact into account, spawning success probability (*w*), which followed a Bernouilly probability distribution with an initial value of 0.5, was added to the model. If the spawning failed, then no juvenile fish survived.

Spatial structure

Space was modelled as a sequence of linear patches (Labonne and Gaudin 2005); there was a varying number of patches (*k*). A patch is a favourable habitat, i.e., there is no other habitat where fish can stay. The initial model included 20 patches (this number corresponded to the maximum number of patches observed on the Beaume population by Issartel and Vincent 1998).

Dispersal

Field results indicate dispersal rates ranging from 5% to 25% per patch, with no directional trend (Labonne and Gaudin 2005). Juveniles and adults were able to disperse. The dispersal rate parameter in the model (*m*) was 0.2 and was constant in the initial model (Table 1). This rate corresponds to the proportion of local density that emigrates from the patch. We allowed movements from each patch to the four nearest neighbour patches (two upstream and two downstream; Fig. 2), because available data did not suggest longer dispersal ranges at the annual scale. The boundary patches, at the upstream or downstream extremes of the population, also emitted beyond the population limit but did not receive any individuals from the outside.

Numerical sensitivity analysis of extinction probability

The demographic growth rate (λ), the measure of population health for deterministic models, was used in our stochastic framework (although it does not rely on the same estimator; Tuljapurkar 1990; Orzack and Tuljapurkar 2001). Elasticity analysis, which quantifies the proportional influence of the life cycle parameters on λ, is now widely applied in conservation biology (Crowder et al. 1994; Kelly and Durand 1999; Bro et al. 2000). Several recent works deal with the accuracy of such elasticity analysis (De Kroon et al. 2000; Heppell et al. 2000; Caswell 2000).

In our case, the growth rate is constrained by density dependence (Strong 1985; Middleton et al. 1995), so it does not fully reflect the health state of the population. Hence, we implemented a numerical sensitivity analysis of the extinction probability instead of a classic sensitivity analysis of the demographic growth rate. Numerical simulations allow us to explore large ranges of parameter variations, and evolution of extinction probability constitutes a good indicator for conservation biologists (Ellner et al. 2002).

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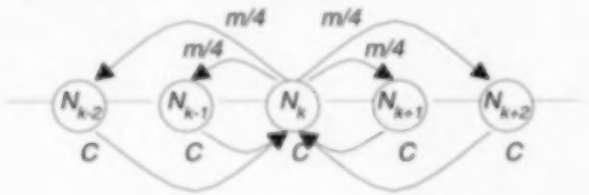
Table 1. Probability distribution, mean and standard deviation (SD) of the parameters in the initial model and range of variation explored in the sensitivity analysis for each parameter of the model.

	Initial model		Sensitivity analysis
Parameters	Probability distribution	Mean (SD)	Minimum–maximum (percent variation)
Adult and juvenile survival rate ($s3$ and $s2$, respectively)	Normal	0.5 (0.02)	0.40–0.56 (20)
Larval survival rate ($s1$)	Log-normal	0.005 (0.001)	0.0025–0.0075 (50)
Fecundity (f)	Log-normal	1200 (300)	1080–1320 (10)
Carrying capacity (C)	Constant	120	30–250 (108)
Spawning success (w)	Bernouilly	0.5	0.4–0.6 (20)
Dispersion rate per patch (m)	Constant	0.2	0–0.4 (100)
Number of patches (k)	Constant	20	1–20

Fig. 2. Spatial structure of the model. Each patch has a density N_k, a carrying capacity C, and a dispersal rate m to the four nearest neighbours.



In the first part of the study, we examined the influence of the intrapatch parameters (adult survival rate, juvenile survival rate, fecundity, carrying capacity, and spawning success) on extinction probabilities (P_e). In the second part, we studied the effects of interpatch structure parameters on P_e (simultaneously the dispersal rate (m) and the number of patch (k)). For each parameter, we computed the model outputs for a given range of variation of the mean parameter. The range was designed to match possible variation observed in wild environment. For example, the influence of adult survival rate $s3$ (initial mean = 0.5) was analysed by computing extinction probabilities for values of mean adult survival rate between 0.45 and 0.55, which is a 10% variation range. Indeed, such a life history parameter may not record high modifications in a given environment. For the dispersal rate m, the variation range was larger (100%, $0 > m > 0.4$), because this parameter may be constrained by natural obstacles or human activities. The range of variation for each parameter is described in Table 1.

Result computing and outputs

The models were built using the program ULM (Ferrière et al. 1996; Legendre and Clobert 1996, http://www.snv.jussieu.fr/Bio/ulm/ulm.html). The initial number of fish in each patch was 30, which is a reasonable assumption regarding average densities observed in the field (10–50 individuals per station). Stochastic models were run using a Monte Carlo method based on time steps over 100 years and 500 trajectories with different algorithm seeds. Extinguished trajectories were not used in the estimation of stochastic growth rate. Population success only relied on their extinction probability over 100 years. The whole population was considered extinct when population size went under $5(k)$ individuals, where k is the number of patches, until $k < 10$. If $k > 10$, then the extinction threshold was 50. A population going under this threshold may have a chance to increase again in reality, but it will be exposed to different mechanisms than those defined in the model. Genetic bottlenecks and consanguinity are likely to accelerate extinction, and the purpose of the population manager will be to maintain a minimal adaptive potential for the population (Hedrick 2001). We also looked at the local temporary extinction rate, which provided an index of patch occupancy (we considered a threshold of five individuals under which the patch became quasi-extinct).

Results

General behaviour of the initial model

All simulations began with a population of 600 fish (30 individuals per patch). Of the simulated population sizes, 95% were lower than 3000 fish after 100 years (Fig. 3*a*), but about 10% were between 2400 and 5000. This range is congruent with field counts (population size estimated between 1000 and 3500 individuals; J. Labonne and P. Gaudin, unpublished data).

The occurrence of several consecutive good spawning years allowed some populations to reach the threshold of density dependence for adults. In the base run, P_e was 0.291, indicating that some simulated populations went extinct before 100 years. The distribution of mean growth rates of populations after 100 years was sharpened around 1 (between 0.94 and 1.03) (Fig. 3*b*) and corresponded to the mean estimates of population growth rates, although variation was lower in the model (Labonne and Gaudin 2005). All available patches were not occupied. Most populations exhibited a large proportion of empty patches (Fig. 3*c*). This point was also consistent with the field observations and seemed to confirm the hypothesis of source–sink structure evocated in a previous study (Labonne and Gaudin 2005).

Impact of intrapatch parameters

The adult survival rate influenced P_e for values under 0.52, and the effect was even more sensitive for values under 0.48. P_e reached 0.77 for a 10% reduction in adult survival rate (Fig. 4). The model was proportionally less influenced by the juvenile survival rate, as a 10% negative variation of this parameter raised P_e to 0.55. However, the slope of extinction probability curve was important, and extinction was certain for values of juvenile survival rate less than 0.0025. On the contrary, values exceeding 0.006 ensured persistence. Fecundity appeared to be the less influent parameter, and a

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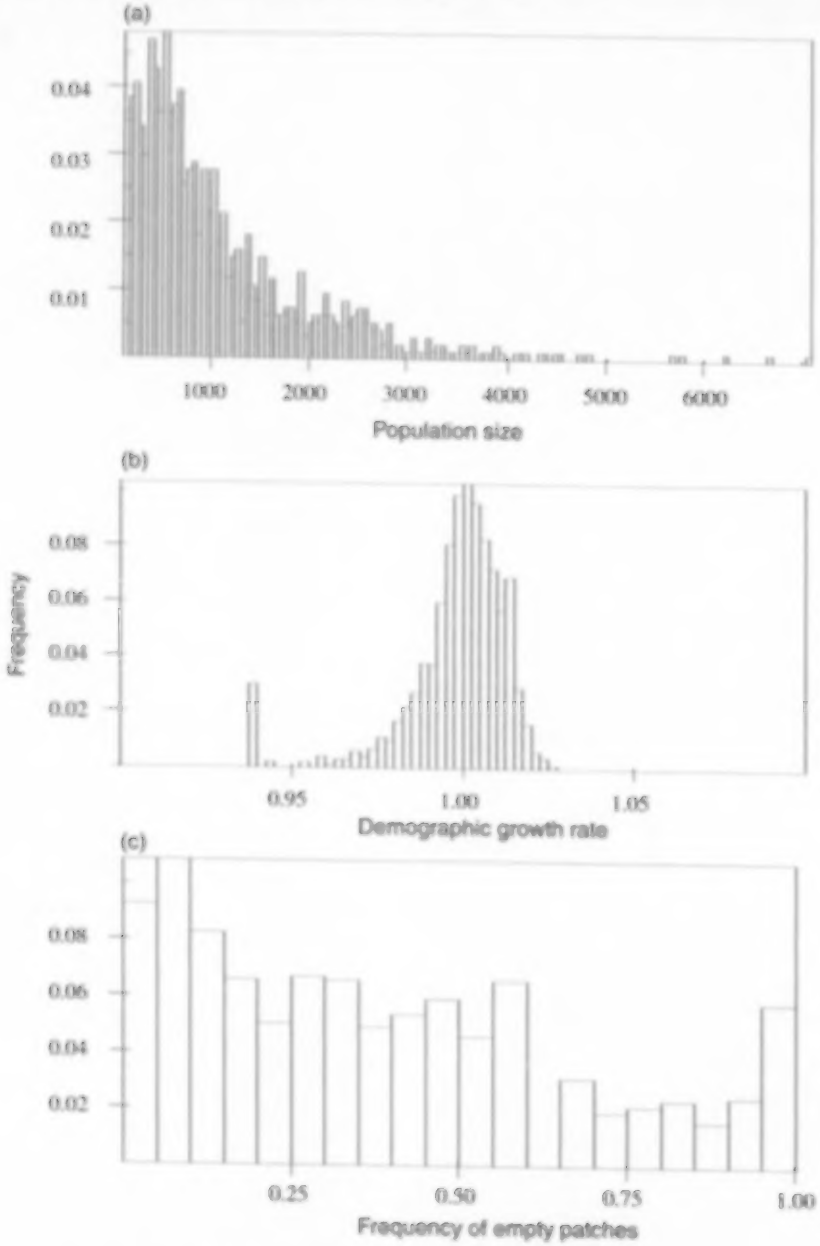
Fig. 3. Frequency distributions for (*a*) the total population size, (*b*) the distribution of the mean stochastic growth rate, and (*c*) the proportion of empty patches after 100 years (Monte Carlo simulation, 1000 trajectories).



10% variation of mean fecundity only increased P_e by a few digits. The carrying capacity (C) showed an effect for value under 100, but high values of C (200) did not ensure the total persistence of the population. The spawning success showed a more important influence on P_e, especially for values under 0.45. For high values (0.6) of spawning success, P_e over 100 years was under 0.1. Therefore, considering these ranges of variation and all other things being equal, we can rank the proportional influence for these parameters:

(adult and juvenile survival) > (larval survival)
> (spawning success = carrying capacity)
> (fecundity)

Impact of interpatch parameters

The number of patches influenced P_e as soon as it went below 15, and the phenomena was stressed under 10 patches (Fig. 5). The role of dispersal was clearly illustrated by these

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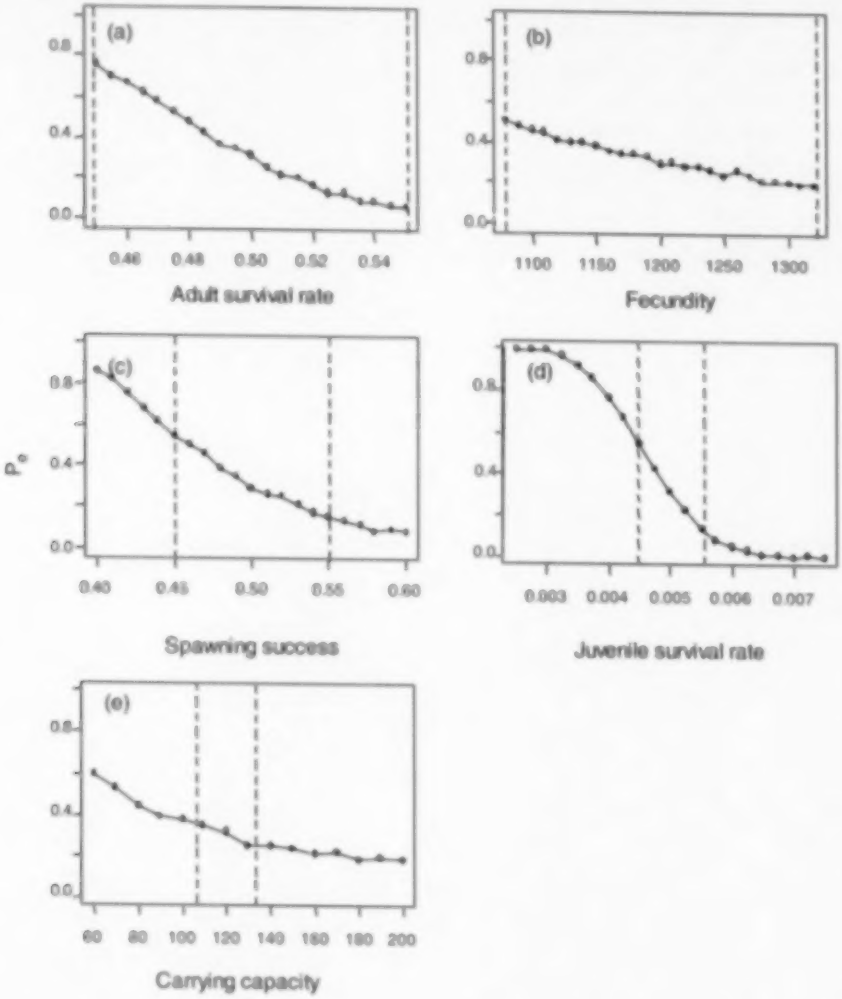
Fig. 4. Plots of the extinction probability (P_e; vertical axis) as a function of (*a*) the adult survival rate, (*b*) the fecundity, (*c*) the spawning success, (*d*) the juvenile survival rate, and (*e*) the carrying capacity (Monte Carlo simulation on 100 years, 500 trajectories). Broken lines indicate the 10% variation range.



results: high rates (> 0.1) were needed to stabilize extinction probability around 0.2. The initial model (with $m = 0.2$) lay above this condition as long as the patch number was sufficient. The results also emphasized the difference between the dispersal rate and the number of habitat patches: the dispersal rate has a threshold effect on P_e, whereas the number of patches has a linear effect on P_e.

Discussion

The role of dispersal at low scale

The estimation of dispersal in a previous study showed that high dispersal events could occur over short distances, and we could not link this phenomenon to any environmental factor (but the assessment in time was limited). Classic metapopulation models assume that dispersal even at low level can ensure population persistence (Levins 1970; Hanski 1999). At lower scale, in the case of the Beaume population, the model outputs showed that low dispersal rates (i.e., <10%) did not allow the persistence and that high dispersal rates were necessary. This result suggests that a fragmented population (i.e., distributed in small patches) requires high levels of dispersal to be able to persist. The theoretical metapopulation results do not apply here, because at this small scale, local abundance in each patch is limited and the number of available patches is small. Also, the linear spatial structure constrains the dispersal: unlike in classic models, there is only one way to travel from one place to another.

Even if dispersal is not a necessary stage of the life cycle in *Z. asper*, it is a necessary function at the population level and should be considered as a plastic behaviour. The model showed frequent local extinction at the patch scale, which is also observed in the field. In classic metapopulation models, all favourable habitats are generally not occupied, and local extinction is viewed as a natural process (Hanski 1999). This

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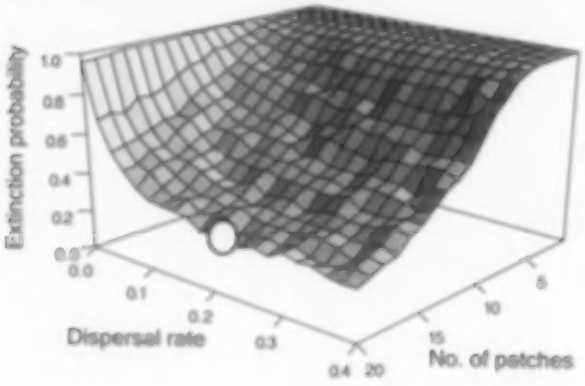
Fig. 5. Extinction probability surface (vertical axis) as a function of the dispersal rate and the number of patches. The open ellipse locates the initial model $m = 0.2$, $k = 20$ (Monte Carlo simulation, 200 trajectories).



result seems to hold true in the present patchy habitat structure. The source–sink functioning hypothesized in the previous demographic study is congruent with the behaviour of this model. The amount of dispersal between patches should also draw attention to the role of unfavourable habitat: in reality, fish may stay a significant time in lower quality habitat (i.e., between patches), hence experiencing different conditions, and this fact may influence their further behaviour, such as mating. Finally, if some individuals live a significant time between favourable patches, then our assessment of the stochasticity on the population may be too pessimistic (for a stochastic event will not have the same impact in different habitats), and we would overestimate P_e. The initial choice for the spatial structure might then be discussed in light of the model's results (Brook 2000). The spatial pattern might be too simplistic for the present case. Precision and realism could be gained by integrating less favourable habitat patches, where spawning could be nearly precluded, for instance, but where survival may not follow the same dynamics as in normal habitat patches. However, the estimation of demographic parameters in these areas in the field remains a challenge because of low numbers, as well as low capturability, of fish in these habitats.

This study demonstrates that the modelling of space at the intrapopulation level is of importance for viability analyses. The interaction between the species life histories (low survival and longevity, few spawning occasions, low density) and the structure of habitat emphasize the role of dispersal in the vulnerability of the population.

Behaviour of the model

When performing a sensitivity analysis in a realistic model, one should be aware that it not only assesses the influence of each parameter on the model outputs, but also gives a clue as to the influence of estimate errors on the model. For instance, we estimated the fecundity parameter from the egg counts of eight females only. The real fecundity may exhibit high variations linked with environment and resources. This limit in our protocol is due to the endangered status of the species: it was not possible to sample more gravid females. Fortunately, in our case, the extinction probabilities are not very sensitive to this parameter, which means that an error on this estimate will not strongly bias the conclusions of the model. The carrying capacity is also difficult to estimate because this parameter depends on the environment and the resource considered. We could only rely on the maximal density observed in a patch in the field. This parameter did not really influence the model results. Contrary to these findings, the spawning success probability seems to influence the extinction probabilities. Observed failure in spawning is not well explained, but its importance in the model shows that further research is needed in this domain. Finally, the model seemed sensitive to larval survival rate, which was calculated with respect to field data (recruitment rate and population stable growth). Real estimates of this parameter are very difficult to obtain, especially in rare fish, and the variability pattern of this parameter remains a major obstacle in population modelling.

Increased temporal variance in demographic parameters could also influence significantly the results. For instance, the model provides growth rates between 0.94 and 1.3: there may be more variation on this parameter in reality. However, preliminary results not included in this study show that inflating the variance for adult survival and fecundity by 100% does not really modify the conclusions. The model is more sensitive to the variance of larval survival rate: inflating this variance by a factor of 2 (which is not unrealistic at first sight) may raise extinction probability from 0.291 to 0.596. In this case, however, the model yields unrealistic densities for young-of-the-year, because the average larval survival is near 0 (0.005) and increased variance leads to many 0 values, as well as generating unexpected high values, which in our model are not counterbalanced by density dependence in juveniles.

The choice of a minimal threshold for the local extinction (here five individuals per patch) assumes that there is an implicit Allee effect in our model, e.g., a minimal density is required to achieve reproduction. This choice can be explained using spatial arguments (for instance, the encounter probability for spawning), but it will directly condition the results of the models for any species that shows low natural density. At very low density, it is likely that our demographic parameters will not reflect the reality. Consanguinity and demographic stochasticity applied to the sex ratio (i.e., absence of male or female) will strongly influence the outcome of the model, but we did not model these mechanisms in this study. Hence, further studies in this field are required (Moller and Legendre 2001), and it is likely that behavioural mechanisms will prevail in these situations. The indicator of patch occupancy also reveals that many patches may be quasi-extinct, although they are considered as available favourable habitats. Such a result is likely to influence predictions made from the habitat model where the quality of a habitat is defined by the local density. Classic modelling approaches may then fail to predict and simulate the dynamics of very low numbers, whereas an individual-based model could be more helpful to link behaviour and population dynamics.

Model limitations

This model cannot be applied safely to simulate and predict the results of a reintroduction protocol for several rea-

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sons. First, some studies report reintroduction costs on the survival rate or the fecundity (Sarrazin et al. 1994), and these costs are not known for *Z. asper* yet. For any planned reintroduction protocol, another study of demographic parameters should be included in order to investigate these potential costs. Second, possible unmeasured variation in environmental factors or in demographic parameters should also be considered (Fieberg and Ellner 2001). Finally, we only considered a linear spatial structure (which matched the structure of the sampling zone), but further predictions should also investigate the case in which the hydrographic network presents a dendritic spatial structure (Fagan 2002).

Another limitation of usual approach in PVA is the absence of life history considerations. PVA models often fail to incorporate probable or demonstrated trade-offs between life histories, e.g., correlation between fecundity and survival or the impact of dispersal on survival. Lack of data or absence of demonstrated correlations partly explain this problem, but it can lead to unrealistic results in PVA models. For instance, in our case, the model predicts that high dispersal rates are necessary for population persistence. If we push the reasoning further, it means that 100% of dispersal is the best strategy to maintain populations. Such predictions are not biologically acceptable. In the light of life history theory, it is now well understood that there are costs associated with behaviours (Roff 1997; Hendry and Stearns 2004). Not only could such an approach improve the realism of PVA models (Freedman et al. 2003), but it could also help conservationists to focus on, for instance, potential evolution in behaviours. Conservationists have to assess the extinction risk, but they should also monitor probability and direction of fast evolutionary processes (Stockwell et al. 2003; Hendry and Stearns 2004). Further investigations are needed in this field for *Z. asper*, especially in the domain of the cost of dispersal, because fragmentation is likely to increase this cost significantly.

It is also important to notice that if the consideration of dispersal in modelling population viability is of primary importance, then the shape of dispersal function can also strongly modify the predictions. In our case, we did not consider long-distance dispersal as no data were available to describe this function, but such a dispersal could quantitatively influence the predicted extinction probability. Moreover, long-distance dispersal could become a crucial point if genetic aspects are to be addressed or if one wants to predict possible colonization of new habitats. Such dispersal is likely to happen at larval stage, which usually remains an unknown in many freshwater fish species (Lucas and Baras 2001). Further research in this domain is needed in *Z. asper*, as well as in other benthic taxa, and should consider genetic tools as a potential way to estimate larval movement rates.

Conservation strategy

We showed that the model was sensitive to different parameters at intra- and inter-patch scales. Classic elasticity analyses are based on life cycle parameters, which are intra-patch parameters, but these parameters cannot all be controlled. It is difficult to imagine how to increase the adult survival rate or the spawning success, based on the current available knowledge. The only conservation measure here would be to limit anthropic impacts on the river (which are already regulated by law), without being able to measure their real effect on fecundity and survival. Now, at the inter-patch scale, connectivity is easier to handle: the anthropic fragmentation is reversible. There is a need to re-establish the continuity of the river to allow fish populations to persist. Dispersal in *Z. asper* can be considered as a resilience mechanism for when problems occur in other demographic parameters. For instance, successive spawning failures can be overtaken if dispersal is high enough. The other lesson is that management or reintroduction protocol should also consider the length of connected river, as well as the number of favourable patches available. Here, the random spawning success, the low density, and the linear structure of the patchy habitat stress the role of spatial components in the persistence of the system. A sustainable strategy for conservation would consider the colonization of restored habitats. These conclusions seem to remain true for larger hydrographic systems (where C would be higher) and should also be considered for other "nonmigratory" fish species (Peter 1998).

The initial model included parameters estimated on the River Beaume. The functioning of this relict population can be assimilated to a boundary population, given the initial distribution area of the species. This population may have adapted to local conditions: population size may have reduced, and genetic bottlenecks may have occurred, allowing the genetic drift to fix potential mutations and, therefore, life histories (Laroche and Durand 2004). The high Mediterranean thermal conditions may explain the low survival (due to faster biological turnover), and this parameter seems to strongly influence the results: the extinction probability for the initial model is about 30%, which is fairly high. The historical distribution area of the species presents other very different kinds of habitat (continental conditions or snowy discharge). It would be wise to plan some reintroductions to reduce the extinction risk by a larger presence area and a variety of habitat conditions. However, these considerations should guide the manager to cautious predictions: there are many biological questions that need to be addressed when considering a local situation. Specific knowledge and expertise are required if one wishes to generalize the present results.

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Appendix A

Let J and A be the number of juveniles and adults in a patch, respectively. Let k be the number of patches. $s3_k$ is the adult survival in patch k and follows a normal distribution:

$$s3_k \rightarrow \mathrm{N}(s3, \sigma(s3))$$

$s2_k$ is the juvenile survival in patch k and follows a normal distribution:

$$s2_k \rightarrow \mathrm{N}(s2, \sigma(s2))$$

sl_k is the survival rate of larva in patch k and follows a log-normal distribution:

$$sl_k \rightarrow \log\mathrm{N}(sl, \sigma(sl))$$

f_k is the fecundity of adults in patch k and follows a log-normal distribution:

$$f_k \rightarrow \log\mathrm{N}(f, \sigma(f))$$

m is the dispersal rate, i.e., the total proportion of individuals leaving a patch. As dispersal is directed towards the four nearest neighbours, each neighbour receives $m/4$ individuals.

Let r be the sex ratio and w be the spawning success. The dynamic in patch k is described following this formula:

$$J_{k,t+1} = A_{k,t} \cdot f_k \cdot r \cdot w \cdot sl_k$$

$$\begin{aligned} A_{k,t+1} = {} & \mathrm{B}(J_k, s2_k(1-m)) + \mathrm{B}(A_k, s3_k(1-m)) \\ & + \mathrm{B}\left(A_{k-2}, s3_{k-2}\frac{m}{4}\right) + \mathrm{B}\left(A_{k-1}, s3_{k-1}\frac{m}{4}\right) \\ & + \mathrm{B}\left(A_{k+1}, s3_{k+1}\frac{m}{4}\right) + \mathrm{B}\left(A_{k+2}, s3_{k+2}\frac{m}{4}\right) \\ & + \mathrm{B}\left(J_{k-2}, s2_{k-2}\frac{m}{4}\right) + \mathrm{B}\left(J_{k-1}, s2_{k-1}\frac{m}{4}\right) \\ & + \mathrm{B}\left(J_{k+1}, s2_{k+1}\frac{m}{4}\right) + \mathrm{B}\left(J_{k+2}, s2_{k+2}\frac{m}{4}\right) \end{aligned}$$

with $\mathrm{B}(n, p)$ as the binomial probability distribution of mean $n \cdot p$ and variance $n \cdot p(1 - p)$.

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Factors influencing summer movement patterns of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*)

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Abstract: We used multiple approaches to study summer movement patterns of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) in the Thomas Fork drainage of western Wyoming, USA. Our objectives were to (*i*) document summer movement patterns of cutthroat trout, especially as related to the concepts of local turnover and displacement distances, (*ii*) determine if fish size and condition were related to mobility, and (*iii*) compare summer movement patterns between years. Large fish (270–384 mm total length) monitored by radiotelemetry showed little movement during the summer as evidenced by a maximum displacement distance of <300 m and a low turnover rate among locations (0.21). For a broad size range of fish marked with visual implant tags (173–390 mm total length) in three study reaches, displacement distances were again low but turnover rate was high (>0.50 in most study reaches). This high turnover rate seemed to be driven mainly by movement among smaller fish as mobility declined with increasing fish size. Mobility also declined with decreasing body condition. Turnover rate in study reaches was higher during the summer of 1999 when stream flows were higher and water temperatures were cooler compared with the summer of 2000.

Résumé : Nous avons utilisé des approches multiples afin d'étudier les patrons estivaux de déplacement de la truite fardée de Bonneville (*Oncorhynchus clarkii utah*) dans le réseau hydrographique de la Thomas Fork dans l'Ouest du Wyoming, É.-U. Nos objectifs étaient (*i*) de décrire les patrons estivaux de déplacement des truites fardées, en particulier en ce qui a trait aux concepts de remplacement local et de distance de déplacement, (*ii*) de voir si la taille et la condition des poissons sont reliées à la mobilité et (*iii*) de comparer les patrons estivaux de déplacement d'une année à l'autre. Les poissons plus grands (de longueur totale 270–384 mm) suivis par radio-télémétrie se déplacement peu pendant l'été, ce qui est confirmé par une distance maximale de déplacement de <300 m et un faible taux de remplacement entre les sites (0,21). Chez des poissons d'une gamme de tailles étendue et marqués avec des étiquettes de type implant visuel (de longueur totale 173–390 mm) dans trois sections d'étude, les distances de déplacement restent faibles, mais le taux de remplacement est élevé (>0,50 dans la plupart des sections). Ce fort taux de remplacement semble s'expliquer principalement par les déplacements des plus petits poissons, car la mobilité est fonction inverse de la taille des poissons. La mobilité décroît aussi proportionnellement au déclin de la condition. Le taux de remplacement dans les sections d'étude était plus élevé à l'été 1999 lorsque les débits étaient plus forts et les températures plus fraîches qu'à l'été 2000.

[Traduit par la Rédaction]

Introduction

Fish movement has important consequences for conservation and management of inland salmonid populations. Seasonal migrations among complementary habitats are required for fish to fulfill different life history requirements (Dunning et al. 1992; Schlosser 1995), and long-distance movements among spawning areas, summer feeding areas, and winter refuge areas have been demonstrated for salmonids (Brown and Mackay 1995; Schrank and Rahel 2004). Human-caused fragmentation of habitats has negative consequences for salmonid populations because it interrupts movement to and from these critical habitats and prevents fish from completing life histories (Rieman and Dunham 2000; Fausch et al. 2002). Less well understood is how human activities may affect fish movements over smaller temporal and spatial scales as fish seek habitats that maximize growth or reduce predation risk (Gowan and Fausch 2002).

An interesting issue for fish ecologists is the extent to which mobility patterns differ among fish species, among

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populations within a species, and even among size classes within a population (Gerking 1959; Gowan et al. 1994; Gowan and Fausch 1996*a*). Recently, much emphasis had been placed on the high degree of mobility evident in some populations of stream fishes (Gowan and Fausch 1996*b*; Kahler et al. 2001). However, Rodriguez (2002) has cautioned that although a high turnover rate of fish within a stream reach is often considered synonymous with high fish mobility, high turnover rate is also compatible with low displacement distances. Thus, there is a need to consider fish movement patterns in terms of both local turnover and the distances that fish move.

Why fish move during summer is not well understood. Movers may be subordinate fish unable to hold a territory (Jenkins 1969), fast-growing fish that have outgrown local food resources (Forseth et al. 1999; Morinville and Rasmussen 2003), fish in poor condition moving to seek increased food resources (Nordeng 1983; Gross et al. 1988; Mesick 1988), or fish moving to find better physical habitat conditions (Mesick 1988; Kahler et al. 2001; Gowan and Fausch 2002). In some situations, mobile fish tend to be longer in total length and lower in body condition than less mobile individuals (Naslund 1990; Gowan and Fausch 1996*a*; Hilderbrand and Kershner 2004). But in other situations, mobility declines with increasing fish size (Hughes 2000).

Determining how fish movement patterns change between years can provide insight into the reasons for movement. The relatively few studies that have examined year-to-year variation in fish movement patterns have emphasized spawning movements and fidelity to spawning sites (Swanberg 1997; Schmetterling 2001). Consequently, information about annual variation in summer movement patterns is limited (but see Hughes 2000). Relating fish movement patterns to abiotic conditions such as stream flow and water temperature would further our understanding of what causes year-to-year differences in fish mobility

The method by which fish movement is studied may influence our perception of mobility patterns (Gowan et al. 1994). For example, radiotelemetry studies, while enabling continuous study of the same individual, usually involve large fish because of concerns about how implanted transmitters may affect the behavior and swimming performance of small fish (Adams et al. 1998). Mark–recapture studies, while facilitating the study of a wide range of sizes, may be limited spatially and involve low sample sizes if recapture rates are low. To avoid these limitations, we used a combination of techniques involving radiotelemetry, mark–recapture of tagged fish, and weirs to examine movement across a large size range of fish present in our study population.

Understanding fish movement within a drainage basin is critical to predicting how human-caused changes to habitat and watershed connectivity will affect movement patterns and population persistence. This is particularly important for inland cutthroat trout throughout the western United States, as many populations have declined as a result of hybridization with nonnatives, habitat degradation, and fragmentation (Young 1995; US Fish and Wildlife Service 2001). Our study took place in the Thomas Fork drainage of Wyoming–Idaho, USA, which contains native populations of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) that are of conservation concern (Binns and Remmick 1994; Schrank et al. 2003).

Our study objectives were to (*i*) document summer movement patterns of cutthroat trout in the Thomas Fork drainage, especially as related to the concepts of local turnover and displacement distances (Rodriguez 2002), (*ii*) determine if fish size and condition were related to fish mobility, and (*iii*) compare summer movement patterns between years to determine if the proportion of mobile fish changed with drought-related declines in streamflow.

Materials and methods

Study site

We studied Bonneville cutthroat trout movement in the upper portions of the Thomas Fork drainage of the Bear River in Lincoln County, Wyoming, and Bear Lake County, Idaho, USA (Fig. 1). Our study site included the Thomas Fork mainstem and three major tributaries: Huff, Little Muddy, and Coal creeks. Climate in this drainage consists of cold, snowy winters and hot, dry summers. Much of the watershed is heavily impacted by livestock grazing, and consequently, there is little riparian vegetation to shade the streams (Binns and Remmick 1994). Mean daily air temperature in summer (June–August) in the region is 15.1 °C based on meteorological data from 1957–2001 for Afton, Wyoming, USA (42°44′N, 110°56′W), approximately 40 km northwest of our study area (www.ncdc.noaa.gov/oa/ncdc.html). Our study took place in 1999 and 2000. Summer air temperatures were close to average during 1999 (mean daily air temperature of 15.5 °C) but were above average for 2000 (mean daily air temperature of 16.1 °C). Water temperatures at the study reaches were higher in 2000 relative to 1999 (Fig. 2). Stream flows within 0.5 km of each study reach were lower in 2000 relative to 1999 (Fig. 2). Within the study area, there were no barriers to fish movement, and thus, fish were free to move among tributaries and the mainstem Thomas Fork.

Objective I: document summer movement patterns of cutthroat trout

We used three approaches to examine movement of Bonneville cutthroat trout within and between tributary streams and the Thomas Fork mainstem during the summers (June–August) of 1999 and 2000. These approaches allowed us to examine movement across a wide size range of fish and consisted of radiotelemetry, marking fish with visual implant (VI) tags (Haw et al. 1990), and use of two-way weirs to catch fish entering or leaving tributary streams.

Radiotelemetry

Between 24 June and 8 July 1999, 12 Bonneville cutthroat trout were captured by electrofishing at sites throughout Coal, Huff, and Little Muddy creeks (Fig. 1). Fish were anesthetized and a radiotransmitter weighing 2.9 g (Advanced Telemetry Systems, Isanti, Minnesota) was surgically implanted into the ventral body cavity of each fish, just anterior to the pelvic girdle (Adams et al. 1998). In all cases, the transmitter weight in air was <2% of the body weight of the fish (Adams et al. 1998). Fish were ground tracked with an Advanced Telemetry Systems R2000 receiver operating at

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Fig. 1. Map of the Thomas Fork drainage of the Bear River in Lincoln County, Wyoming, and Bear Lake County, Idaho. Circles indicate the locations of 12 fish implanted with radiotransmitters and tracked during the summer of 1999. The displacement distances of these 12 fish did not exceed 300 m. Numbers inside the circles indicate fish identification numbers as shown in Table 1. The location of weirs on Coal and Huff creeks and the locations of three study reaches where three-pass electrofishing was done are also shown.

frequencies of 150.000–151.999 MHz and a four-element Yagi antenna. Fish were disturbed occasionally to determine if they were still alive. All fish were alive at the end of the tracking period. The 12 fish were located every other day throughout the summer from early July through mid-August. The average total length of these fish was 313 mm (range 270–384 mm) and average weight was 303 g (range 187–491 g) (Table 1). Turnover rate was calculated as the proportion of time that fish were found in a location different from the previous location. Summer displacement distance for each radiotransmitter-implanted fish was determined as the total distance moved from the most upstream to the most downstream location.

Weirs

We installed two-way weirs in Coal and Huff creeks to monitor fish movement into and out of these tributaries. The weirs allowed us to determine if fish that were VI tagged in the three study reaches (described above) moved among tributaries. Furthermore, we implanted VI tags in all fish captured in the weirs to determine if these fish might later move into the three study reaches. Weir design followed Gowan and Fausch (1996*b*). Weirs included 0.5 m of skirting that was buried in the substrate or bank and then covered with sediment and rocks to ensure that fish were unable to escape around the weir. The Huff Creek weir was operated from 4 June through 22 August 1999. The Coal Creek weir was operated from 23 July through 22 August 1999. The weirs were monitored at least every other day to determine if fish were moving upstream or downstream. Fish captured in the weirs were measured, weighed, implanted with a VI tag, and released in the direction they were traveling. The weir was able to capture fish having a total length ≥150 mm.

VI tags

During the summers of 1999 and 2000, we monitored the movement of fish into and out of three study reaches in Coal and Huff creeks that were representative of habitat throughout the tributaries (Fig. 1). The three study reaches were intensively electrofished (three-pass depletion with a backpack electrofisher) three times each summer in June, July, and August. Block nets were placed at the upstream and downstream ends of each study reach during electrofishing. Study reach length was 160 m in upper Coal Creek, 200 m in mid-

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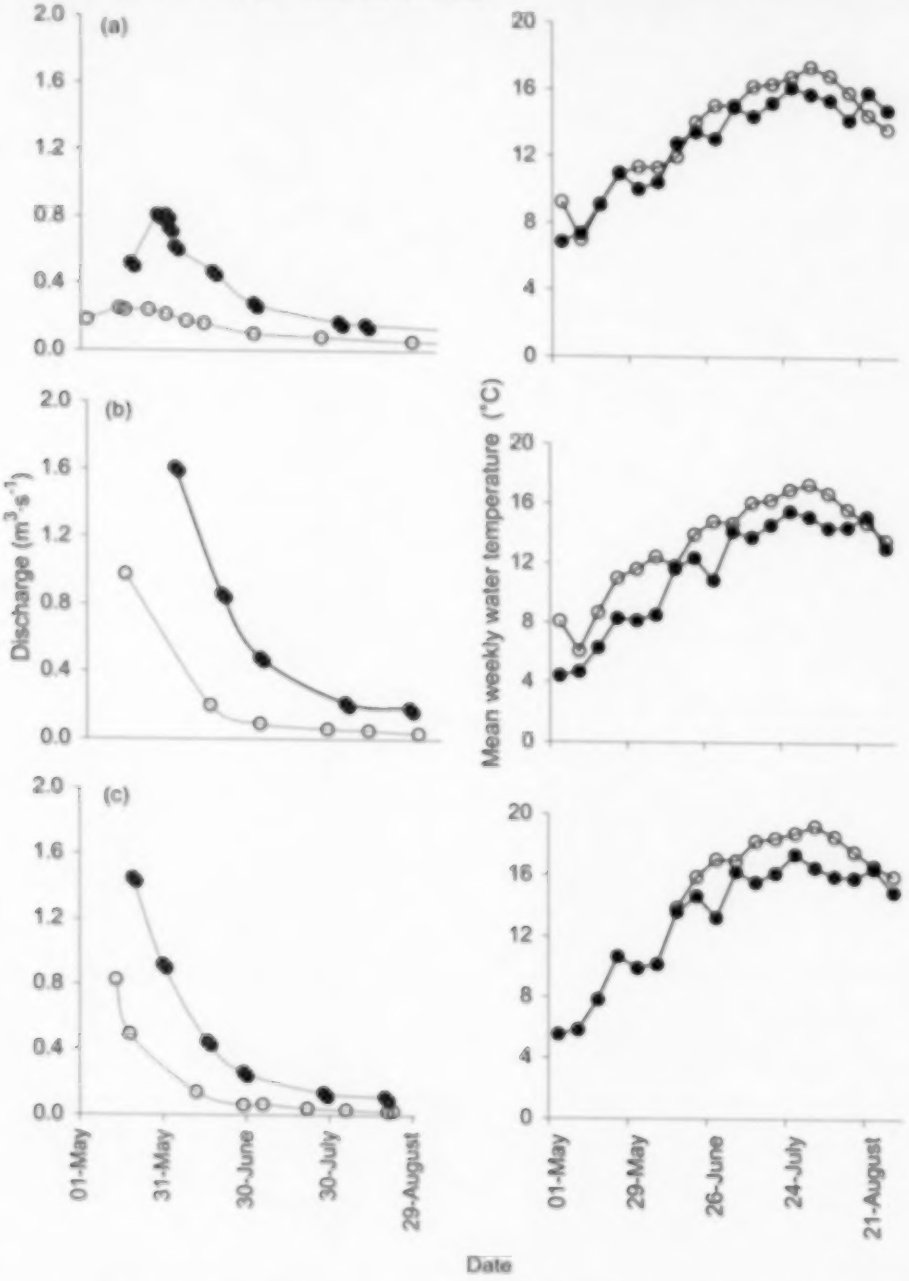
Fig. 2. Stream discharge (left panels) and water temperature data (right panels) for (*a*) Huff Creek, (*b*) lower Coal Creek, and (*c*) upper Coal Creek. Solid circles are 1999 data; open circles are 2000 data.



dle Coal Creek, and 214 m in Huff Creek. During each sampling, all unmarked Bonneville cutthroat trout >150 mm were marked with a unique alphanumeric VI tag (Haw et al. 1990), measured, weighed, and released in the same reach. A total of 151 fish were VI tagged in the three study reaches during the summers of 1999 and 2000. We also clipped the adipose fin of each VI tagged fish to monitor tag loss. All fish captured that had been previously marked with a VI tag were also measured, weighed, and released. Fish that were marked with a VI tag and then recaptured in the same reach during the subsequent sampling period were considered recaptures, and fish >150 mm captured in a reach without a VI tag or with a VI tag from another reach were considered immigrants. We also considered fish to be immigrants if they

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Table 1. Data for 12 fish that were implanted with radiotransmitters and tracked during summer 1999.

Fish ID	Original location of capture and release	Fish length (mm)	Fish weight (g)	Tracking date		No. of times a fish was located	Displacement distance (m)	Turnover rate
				Initial	Final			
1	Lower Coal Creek	384	491	8 July	18 Aug.	14	200	0.23
2	Lower Coal Creek	335	393	12 July	18 Aug.	13	100	0.25
3	Middle Coal Creek	320	272	12 July	19 Aug.	14	<100	0.25
4	Middle Coal Creek	332	381	2 July	17 Aug.	13	<100	0.00
5	Upper Coal Creek	286	247	10 July	19 Aug.	12	<100	0.09
6	Upper Coal Creek	303	290	10 July	19 Aug.	12	<100	0.09
7	Upper Huff Creek	275	252	9 July	19 Aug.	13	100	0.36
8	Upper Huff Creek	298	262	7 July	19 Aug.	15	300	0.40
9	Lower Huff Creek	270	187	9 July	18 Aug.	13	300	0.08
10	Lower Huff Creek	316	261	9 July	18 Aug.	13	200	0.18
11	Little Muddy Creek	321	333	2 July	19 Aug.	17	100	0.31
12	Little Muddy Creek	316	264	2 July	19 Aug.	17	100	0.27

Note: Displacement distance indicates the distance from the most upstream to the most downstream location of a fish over the entire tracking period. Turnover rate was calculated as the proportion of time that a fish was found at a location that was different from its location on the previous tracking date.

had been tagged in a study reach, not captured for one or more sampling periods, but then recaptured in the study reach at a later date. These fish had probably moved out of the study reach and then returned. It is unlikely that they were present but missed during sampling because our capture efficiency was high (see Results: Objective I). During each sampling effort, numbers of recaptured and immigrant fish (>150 mm) were recorded.

We could use VI tags only on fish >150 mm because fish below this size had poor tag retention. Therefore, it is possible that smaller fish could have grown enough to exceed 150 mm between sampling periods and thus been counted as unmarked fish when in reality they would have been present but too small to mark during the previous sampling period. To avoid this bias, we determined growth rate during the summer for fish captured at each study reach and eliminated fish during each sampling period that could have grown into the markable length category (>150 mm) since the last sampling effort (details in Schrank 2002). After eliminating these fish, we had 78 immigrant fish and 38 recaptured fish for our analysis.

To determine how frequently fish were moving in and out of the three study reaches, we calculated turnover rate during the July and August sampling periods in 1999 and 2000. Turnover rate was calculated as the 1 minus the proportion of marked individuals (Rodriguez 2002) in each reach during each sampling period.

Objective II: determine if fish size and condition are related to mobility

To determine if propensity to move into or out of a study reach was related to fish size, we compared total lengths of immigrant and recaptured fish among study reaches using a two-way ANOVA with movement status (recaptures or immigrants) and site as factors.

To determine if movement status was related to fish condition, we compared relative weights (W_r) for all immigrant and recaptured fish. The W_r was calculated based on the equation for standard weight for lotic cutthroat trout proposed by Kruse and Hubert (1997): $\log_{10}$(standard weight (g)) = –5.189 + 3.099 $\log_{10}$(total length (mm)). Of the 116 immigrant and recaptured fish, there was one fish for which a weight was not recorded; therefore, we used only 115 fish for this analysis. The W_r values were compared using a two-way ANOVA with movement status and site as factors. The Bonferroni procedure was used for post hoc comparisons among study reaches.

Objective III: compare summer movement patterns between years

To determine whether the turnover rate, and thus movement frequency, changed from 1999 to 2000, we calculated the mean difference between the turnover rate in 2000 and 1999 for the three study reaches. The data from July and August of a given year at a given site were pooled in this analysis. We then calculated a 95% confidence interval around the mean difference in turnover rate. If this confidence interval did not include zero, it would indicate a difference in the turnover rate between the two years. A difference in turnover rate would, in turn, indicate a difference in movement tendencies between years.

Results

Objective I: document summer movement patterns of cutthroat trout

Radiotelemetry data indicated that large fish (range 270–384 mm total length, average 313 mm) were not moving over long distances during the summer. The 12 fish implanted with radiotransmitters had displacement distances ≤300 m (Table 1; Fig. 1). Furthermore, average turnover rate was relatively low, at 0.21, indicating that 79% of relocated individuals were within the same pool where they had been found on the previous tracking date (Table 1).

Catches in weirs also indicated little long-distance movement of Bonneville cutthroat trout. No fish moved upstream and four fish (range 181–266 mm total length, average 217 mm) moved downstream through the Coal Creek weir during the 31 days that it was in operation. Seven fish moved upstream and 10 fish moved downstream through the Huff

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Table 2. Turnover rate of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) captured in three study reaches.

	Year		
Study reach	1999	2000	Difference in turnover rate[a]
Huff Creek	1.00 (n = 11)	0.59 (n = 32)	0.41
Lower Coal Creek	0.92 (n = 13)	0.54 (n = 24)	0.38
Upper Coal Creek	0.77 (n = 26)	0.30 (n = 10)	0.47

Note: Turnover rate was calculated as 1 minus the proportion of marked individuals (Rodriguez 2002). The total number of fish collected in the sample reaches (n) is given in parentheses.
[a]The mean difference in the turnover rate between years 1999 and 2000.

Creek weir during the 79 days that it was in operation (range 193–410 mm total length, average 261 mm). None of the fish given VI tags in the three study reaches were found in the weirs. Likewise, none of the fish given VI tags in the weirs were found in any of the study reaches. This suggests that fish moving out of the upper Coal Creek study reach did not move downstream more than 4.2 km, which was the distance to the weir, and likewise, fish moving out of the Huff Creek study reach site did not move downstream more than 0.5 km, the distance to the weir (Fig. 1). The weirs could catch fish as small as 150 mm total length, which indicates that the absence of long-distance movement observed in large fish using radiotelemetry was also true for smaller fish.

VI tagging data indicated that of the 116 fish used in our analysis, 78 were immigrants and 38 were recaptures (range 173–390 mm total length, average 226 mm). Our tag loss rate was 1%; therefore, it was unlikely that immigrants were fish that had lost their VI tag. Turnover rate was 0.5 or greater at all sites except in upper Coal Creek during 2000 (Table 2). Despite the high turnover rate in the study reaches, displacement distances were low, as VI tagged fish were never observed to move among the three study reaches, nor were they ever caught in the downstream weirs on Coal and Huff creeks.

We were confident that we captured most fish in a reach during a given sampling period because capture probabilities for each pass of the three-pass depletion electrofishing were high (capture probabilities were >0.7 for over 70% of the passes). Capture probabilities were calculated using the program Microfish 3.0 (Van Deventer and Platts 1989). Therefore, unmarked fish likely represented fish that had moved into the study reaches since the last sampling period rather than fish that had not been captured during the last sampling effort. Furthermore, to determine if movement in or out of study reaches was causing increases or decreases in populations over the summer, we also calculated abundance estimates and 95% confidence intervals (for fish >150 mm) during each of the six sampling periods (Microfish 3.0; Van Deventer and Platts 1989). Abundance estimates showed no consistent increase or decrease throughout the summer, indicating that both emigration and immigration were occurring in the three study reaches (Schrank et al. 2003).

Another concern was whether the failure to recapture fish previously marked in a reach was due to mortality rather than emigration. There were 14 fish for which capture histories indicated that individuals were likely to be moving out of study reaches rather than experiencing mortality within them. Seven of these fish were initially given VI tags in one of the three study reaches, were subsequently absent from the reach, but then were recaptured in the same reach at a later time (fish Nos. 1–7 in Table 3). As an example, consider fish No. 4 that was initially captured and given a VI tag during preliminary sampling in lower Coal Creek in August of 1998. This fish was not present in the study reach in June 1999, was present in July 1999, was absent in August 1999, and was present in June 2000. This means that the absence of the fish in June 1999 and August 1999 was not due to mortality but to the fish having left that study reach. Because of other studies occurring in this drainage, fish were being marked at other sites within the watershed in addition to our three study reaches. As a result, five fish that were initially marked elsewhere were subsequently captured in one of the study reaches (fish Nos. 8–12 in Table 3) and two fish that were initially marked in one of the study reaches were subsequently captured elsewhere in the drainage (fish Nos. 13 and 14 in Table 3). For example, fish No. 10 was initially found upstream of the study reach in June of 1999 and was not found in the study reach in July and August of 1999 or June of 2000 but moved into the study reach and was captured there in July and August of 2000. These recapture histories provide evidence that some fish not recaptured in the study reaches were moving rather than dying.

Objective II: determine if fish size and condition are related to mobility

Fish that remained in the study reaches (recaptures) were significantly longer than immigrant fish (two-way ANOVA, df = 115, F = 5.67, p = 0.019, α = 0.05). Mean length ± 1 SE was 239 ± 7 mm for recaptured fish and 220 ± 5 mm for immigrant fish. There was no interaction between site and movement status (F = 0.65, p = 0.526) and no effect of site on fish length (F = 2.10, p = 0.127).

Recaptured fish had significantly lower condition than immigrant fish as measured by W_r (two-way ANOVA, df = 114, F = 10.03, p = 0.002, α = 0.05). Mean (±1 SE) W_r across all sites for recaptured fish was 83.4 ± 1.2 and for immigrant fish was 88.1 ± 0.9. There was no interaction between movement status and site (F = 0.16, p = 0.849). Mean W_r among study reaches differed (F = 9.25, p < 0.001). Post hoc comparisons indicated that fish (immigrants and recaptures combined) from the upper Coal Creek site had a significantly higher average W_r (±1 SE) (90.3 ± 1.3) than fish from both lower Coal Creek (82.9 ± 1.3, p < 0.001) and Huff Creek (84.0 ± 1.3, p = 0.005).

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Table 3. Capture histories of 14 fish marked with VI tags in the Thomas Fork system.

Study reach	Fish ID	Location status by date						
		Aug. 1998	June 1999	July 1999	Aug. 1999	June 2000	July 2000	Aug. 2000
Fish that were marked in a study reach, moved out of it, and then returned								
Huff Creek	1	NA	NA	+	□	+	□	□
Lower Coal Creek	2	+	□	□	+	□	□	□
Lower Coal Creek	3[a]	+	+	+	□	□	□	□
Lower Coal Creek	4	+	□	+	□	+	□	□
Lower Coal Creek	5	+	□	□	+	+	+	+
Lower Coal Creek	6	NA	NA	NA	NA	+	□	+
Upper Coal Creek	7	+	□	□	+	□	□	□
Fish that were marked outside a study reach and then moved into it								
Huff Creek	8	NA	▽	□	+	□	□	□
Upper Coal Creek	9	NA	▽	+	□	□	□	□
Upper Coal Creek	10	NA	▽	□	□	□	+	+
Upper Coal Creek	11	NA	▽	+	□	□	□	□
Upper Coal Creek	12	NA	▽	▽	+	□	□	□
Fish that were marked in a study reach and subsequently captured elsewhere								
Huff Creek	13[b]	NA	+	□	□	□	□	□
Upper Coal Creek	14	NA	+	□	□	▽	□	□

Note: + indicates that a fish was captured within a study reach; □ indicates that a fish previously captured in the study reach was absent from that reach during a subsequent sampling period; ▽ indicates that a fish was captured elsewhere in the basin outside the three study reaches; NA, not available.
[a]Fish No. 3 was captured in the study reach during sampling for another study in October 1999.
[b]Fish No. 13 was captured outside the study reach during sampling for another study in October 1999.

Objective III: compare summer movement patterns between years

The turnover rate among the three study reaches was always higher in 1999 than in 2000 (Table 2). The mean difference in the turnover rate between years 1999 and 2000 was 0.42 and the 95% confidence interval for this difference did not include zero ($0.31 < 0.42 < 0.53$). Therefore, turnover rate was substantially higher in 1999 than in 2000, indicating that fish were less mobile in 2000 (Table 2).

Discussion

Summer movement patterns of Bonneville cutthroat trout were characterized by low displacement distances and low turnover rates for large fish implanted with radiotransmitters (average total length 313 mm) but low displacement distances and high turnover rates for a broader size range of fish implanted with VI tags (average total length 226 mm). These results support the concept that fish mobility needs to be considered in terms of both attributes because high turnover at a local scale is compatible with relatively short movement distances (Rodriguez 2002). It is interesting to consider how our perception of mobility in fish populations is influenced by the interaction of turnover rate and movement distances. Turnover rate and displacement distance can be considered as axes that define a range of mobility types (Fig. 3). At one extreme are fish populations that show little mobility because few individuals leave a local site and those that do generally only move a short distance. Examples of such populations may be centrarchids in streams (Gerking 1959), fish with limited mobility such as sculpin (Petty and Grossman 2004), or the large Bonneville cutthroat trout implanted with radiotags in our study. At the other extreme are populations where most individuals are constantly moving over large distances. Pelagic ocean predators such as tunas (Block et al. 2005) or bull trout in larger rivers (Swanberg 1997; Bahr and Shrimpton 2004) might be examples of highly mobile fish. Characterizing the mobility for other

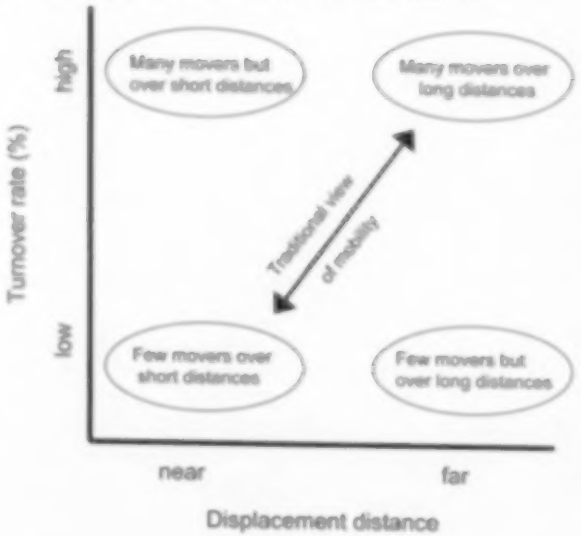

Fig. 3. Turnover rate and displacement distance can be considered as axes that define a range of mobility types. Traditionally, mobility has been viewed along a diagonal axis that confounds these factors. Low mobility was characterized as few individuals moving short distances, and high mobility was characterized as many individuals moving long distances. However, many stream salmonid populations seem to have many individuals (high turnover) moving over short distances (low displacement).

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combinations of turnover and displacement distance is more difficult. Many inland populations of stream salmonids show a high turnover rate but low displacement distance such as that observed in the Bonneville cutthroat trout marked with VI tags in our study (Rodriguez 2002). Fish ecologists have tended to consider such populations as being highly mobile because the emphasis has been on turnover rate rather than how far fish actually move (Gowan and Fausch 1996*a*). It is difficult to think of fish populations that occupy the portion of mobility space characterized by low turnover but high displacement distances for the few individuals that do move. In terrestrial systems, examples would be highly territorial species such as cougars (Sweanor et al. 2000) or wolves (Gese and Mech 1991) where young are forced to disperse great distances to find unoccupied territories. A challenge for fish ecologists will be to consider how movement patterns for various species can be characterized in terms of both the proportion of individuals that leave a reach (i.e., turnover) and the average distances moved by such individuals (i.e., displacement distance).

High turnover but short movement distance is a common pattern for stream salmonids in summer (Gowan and Fausch 1996*a*; Hilderbrand and Kershner 2000; Rodriguez 2002). Such movement is best characterized as ranging behavior whereby organisms leave their current habitat and seek similar habitats with better resources in nearby areas (Dingle 1996). For salmonids, summer ranging behavior is thought to be associated with monitoring habitat conditions and maximizing foraging opportunities (Gowan and Fausch 2002). Stream salmonids often show increased local movements to meet increased metabolic demand as food resources are reduced (Fausch et al. 1997; Forseth et al. 1999; Morinville and Rasmussen 2003). The energetic profitability of stream locations varies with changes in streamflow and invertebrate drift (Gowan and Fausch 2002), which may explain why high turnover but low displacement distance is prevalent in drift-feeding stream salmonids.

In our study, the tendency to move declined with fish size as evidenced by the frequency with which radiotransmitter-implanted fish were detected in the same pools throughout the summer (low turnover rate) and by the fact that for VI tagged fish, recaptures were significantly larger than immigrants ($p = 0.019$). Hughes (2000) suggested that because larger fish generally occupy the most energetically profitable locations in a stream, they should move least and his data on movement of Artic grayling (*Thymallus arcticus*) ranging from 150 to 410 mm total length supported this hypothesis. This does not seem to be the case for Bonneville cutthroat trout in the Thomas Fork. Fish that did not move between periods were in poorer condition than fish that moved. This does not support the idea that large fish were simply staying put in energetically profitable locations. Tributaries to the Thomas Fork tend to have few deep pools in the summer, at least partly because past livestock grazing has reduced riparian vegetation, increased erosion, and reduced bank stability (Binns 1981; Binns and Remmick 1994). Therefore, large cutthroat trout may have fewer habitat options and tend to remain in the few large pools that are present even if food levels decline. Supporting the idea that large fish were severely habitat limited in the Thomas Fork is the observation that turnover rate within study reaches was lower in 2000 than in 1999 in association with lower stream flow. This decrease in flow would have the effect of reducing habitat for larger fish as the number and depths of pools declined, restricting fish movement even further.

We found that large cutthroat trout tended to be located in the same pool throughout the radiotelemetry study, but we only located fish during the day. We do not know the extent to which large Bonneville cutthroat trout may make nocturnal ranging movements to explore habitat conditions in other areas of a stream. However, Young et al. (1997) reported that another subspecies, Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*), was largely inactive at night. More work is needed to understand how stream salmonids assess the quality of habitat conditions in other areas of the stream.

Water temperature is another factor that could influence movement patterns. In some cases, salmonids move to cold-water refuge areas when remaining areas of a stream become too warm (Berman and Quinn 1991; Li et al. 1994; Nielsen et al. 1994). However, in the Thomas Fork drainage, Bonneville cutthroat trout remain in tributaries during the summer even when daytime water temperatures reach 27 °C (Schrank et al. 2003). The short duration of these high water temperatures, which last only a few hours during each diel cycle, may allow fish to tolerate them until thermal conditions improve (Johnstone and Rahel 2003; Schrank et al. 2003).

The lack of movement by larger fish in this watershed suggests that an effective management action would be a restoration of habitat to increase pools. Historically in these tributaries, beaver ponds were common and likely provided pool habitat for large fish; however, with increases in grazing and an absence of willows, beaver are less common (Binns 1981). Binns and Remmick (1994) examined Bonneville cutthroat trout populations before and after habitat improvement on Huff Creek. They found that large cutthroat trout (>15 cm) increased from 22 trout·km^{-1} before habitat improvement to 106 trout·km^{-1} 11 years after habitat improvement. This suggests that habitat limits the abundance of large fish in the tributaries and this would be especially true in dry years.

Movement studies often employ a single method to examine fish movement and this can affect the conclusions drawn from these studies when the size of fish studied is limited by the method used. For example, studies that use radiotelemetry can only monitor movements of fish large enough to accommodate implantation of transmitters (Adams et al. 1998). Thus, movement by smaller fish needs to be assessed by other techniques. We examined movement patterns of relatively large fish (>275 mm) with radiotelemetry and relatively small fish (>150 mm) using VI tags and weirs. If we had only used radiotelemetry, we might have concluded that Bonneville cutthroat trout moved little during the summer (low turnover rate) and often resided in the same pool for extended periods. However, if we had only used VI tag recapture data, we would have concluded that Bonneville cutthroat trout moved frequently because turnover rate was high.

Using multiple approaches to study movement provided a more complete picture of the movement patterns of Bonneville cutthroat trout in the Thomas Fork system. A proportion of the adult population undergoes extensive migrations in the spring to headwater tributaries to spawn and then back

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to mainstem reaches to spend the summer (Schrank and Rahel 2004). The relatively few large fish that remain in the tributaries show little movement throughout the remainder of the summer, often residing in the same pool for extended periods. Smaller fish show frequent local movement during the summer with high turnover within a reach but have low displacement distances and tend to remain within the tributary streams. This size difference in summer movement patterns probably reflects a greater habitat limitation for large fish relative to small fish. Future studies will benefit from considering turnover and displacement as distinct aspects of fish movement as we attempt to understand the reasons for the diversity of movement patterns evident in stream fishes. A focus on understanding the extent, timing, and causes of movement across the size range of fish in a population will allow researchers to better predict how human changes to a watershed, such as habitat degradation, fragmentation, and water diversion, will affect movement patterns and population persistence.

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Effects of recreational and commercial fishing on blue sharks (*Prionace glauca*) in Atlantic Canada, with inferences on the North Atlantic population

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Abstract: The nominal catch of blue sharks (*Prionace glauca*) reported for the Canadian Atlantic grossly underestimates the annual catch mortality of about 1000 tonnes (t), making blue sharks the most frequently caught large shark in Canadian waters. Although blue sharks accounted for 99% of all sharks landed at recreational shark fishing tournaments, tournament catches accounted for only 3% of total fishing mortality. Standardized catch rate indices suggested a decline in blue shark abundance of about 5%–6%·year^{-1} since 1995. An increased mortality rate in recent years was suggested by a decline in the median size of blue sharks in the commercial catch. Two independent calculations suggest that North Atlantic catches exceeded 100 000 t, with catch mortalities ranging between 26 000 and 37 000 t. Because tagging studies indicated that blue sharks are highly migratory with a single population in the North Atlantic, the Canadian contribution to overall population mortality accounts for only 2% of the total. The fact that blue shark populations are relatively productive and resilient may help explain their persistence in the face of high international catch mortality and a decline in relative abundance.

Résumé : Les captures nominales de requins bleus (*Prionace glauca*) signalées dans l'Atlantique canadien sous-estiment considérablement la mortalité annuelle due à la pêche d'environ 1000 tonnes (t); il s'agit donc du grand requin le plus couramment capturé dans les eaux canadiennes. Bien que les requins bleus représentent 99 % de tous les requins débarqués lors des tournois récréatifs de pêche au requin, les captures lors des tournois ne représentent que 3 % de la mortalité totale due à la pêche. Les indices standardisés du taux de capture indiquent un déclin de l'abondance des requins bleus d'environ 5–6 %·an^{-1} depuis 1995. La diminution de la taille médiane des requins bleus dans les captures commerciales laisse croire à une augmentation du taux de mortalité au cours des années récentes. Deux calculs indépendants indiquent que les captures en Amérique du Nord dépassent 100 000 t et que les mortalités dues à la capture sont de l'ordre de 26 000 à 37 000 t. Comme des études de marquage indiquent que les requins bleus migrent beaucoup et qu'ils forment une seule population dans l'Atlantique Nord, la contribution canadienne à la mortalité globale de la population représente seulement 2 % du total. La persistance des requins bleus malgré une capture internationale importante et un déclin de leur abondance relative s'explique peut-être par la productivité relativement élevée et la résilience des populations.

[Traduit par la Rédaction]

Introduction

The blue shark (*Prionace glauca*) is a large temperate and tropical pelagic shark species of the family Carcharhinidae that occurs in the Atlantic, Pacific, and Indian oceans. The species is highly migratory, with tagging results suggesting that there is a single well-mixed population in the North Atlantic (Casey and Kohler 1991). In Canadian waters, the blue shark has been recorded off southeastern Newfoundland, the Grand Banks, the Gulf of St. Lawrence, and the Scotian Shelf, and in the Bay of Fundy. At certain times of the year, it is probably the most abundant large shark species in eastern Canadian waters (Templeman 1963).

The inherent vulnerability of sharks and other elasmobranchs to overfishing and stock collapse is well documented. The International Plan of Action for the Conservation and Management of Sharks (The Food and Agriculture Organization of the United Nations (FAO) 1998) concluded that many of the world's shark species are severely depleted. A recent policy statement by the American Fisheries Society noted that most elasmobranch populations decline more rapidly and recover less quickly than do other fish populations (Musick et al. 2000). Indeed, numerous authors have noted the low productivity of elasmobranchs compared with teleosts, which is largely a result of their low fecundity and late age of sexual maturation (Cortés 1998; Smith et al. 1998).

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Although the blue shark is probably the most frequently caught large shark in the world's oceans (Walker 1998; Stevens et al. 2000), the health of the blue shark population has never been properly assessed. Based on an analysis of US pelagic longline logbook information from vessels fishing in the Northwest Atlantic, Baum et al. (2003) suggested that the North Atlantic population had declined by 60% since 1986. In contrast, an initial attempt to prepare a North Atlantic wide stock assessment of blue sharks suggested that there had been no decline in population numbers since 1971, although the report noted that the assessment was hampered by poor data quality, making the conclusion very provisional (International Commission for the Conservation of Atlantic Tunas (ICCAT) 2005). In the Canadian Atlantic, the unreported bycatch of blue sharks is estimated to be about 100 times larger than the reported catch (Campana et al. 2002*a*). The status and health of the blue shark population and fishery in Canadian waters has never been evaluated, and the impact of the reported and unreported catches on the population is unknown.

Since 1995, fisheries management plans in Atlantic Canada have maintained nonrestrictive catch guidelines of 250 tonnes (t) annually (not based on estimates of stock abundance) for blue sharks in the directed shark fishery (Campana et al. 2002*a*). Fishing gears permitted in the directed commercial fishery are limited to longline, handline, or rod and reel gear. The recreational fishery is restricted to rod and reel (hook and release) only. No catch restrictions were put on sharks caught as bycatch in large pelagic fisheries. A ban on "finning" sharks (the removal of the fins and at-sea disposal of the finless carcass) was implemented in June 1994.

Blue sharks in Atlantic Canada are incidentally caught in large numbers by commercial fishers and are increasingly being targeted by recreational shark fishers through fishing tournaments. The objective of this study is to provide an initial view of the impact of these fishing pressures on the status of the blue shark population, both within Canadian waters and in the North Atlantic as a whole. The analysis begins with a reconstruction of the total blue shark catch, including discards, in both the commercial and recreational fishery. Indices of abundance and exploitation rate were calculated from analyses of standardized catch rates, tag recaptures, and length composition. The Canadian catch mortality estimates were then put into the broader context of the entire North Atlantic population.

Materials and methods

Length and maturity data

Length and weight were measured and sexual maturity was assessed in examinations of more than 2000 blue sharks landed at shark tournaments. The standard length measure reported in this paper is that of fork length measured over the curve of the body. Alternate measures of length used by observers or the fishing industry were standardized to curved fork length using a series of interconversion factors developed through matched measurements made by scientific staff on freshly caught blue sharks (Campana et al. 2004). Length at maturity varied between 193 and 210 cm for males, with a length at 50% maturity of 201 cm (Campana et al. 2004). Mature females were seldom caught at shark tournaments, so length at maturity could not be estimated. However, reports from the literature indicate that females reach sexual maturity at lengths greater than 185 cm (Pratt 1979).

Length composition in the commercial catch was determined from observer measurements from both the Scotia–Fundy and Newfoundland Observer Programs. Trends in median length through time were plotted using locally weighted least square regressions (LOESS). To minimize seasonal differences, the analysis was restricted to the fall and winter seasons.

Tagging studies

The migration pattern and exploitation rate of blue sharks in Canadian waters were analyzed on the basis of tag recaptures from two sets of tagging studies. A total of 2017 tags were applied to blue sharks in a Canadian tagging program carried out between 1961 and 1980, 17 of which were recaptured (Burnett et al. 1987). A second tagging study was carried out by the US National Marine Fisheries Service (NMFS) in cooperation with Canadian fishers. This study applied thousands of tags to blue sharks in US and international waters, 916 of which were applied in Canadian waters between 1971 and 2002. A total of 59 of the Canadian-tagged sharks were subsequently recaptured, 17 of which were in Canadian waters. Both studies used steel dart tags inserted into the dorsal musculature behind the first dorsal fin. Recapture details are reported in Campana et al. (2004).

Commercial landings and observed bycatch

Commercial catch and effort statistics were available for the period of 1979 to the present, with the landings from 1994 onwards considered to be very reliable. Canadian landings data were extracted from Department of Fisheries and Oceans (DFO) zonal statistics files (ZIF) from 1991–2002 and from DFO MARFIS statistics files for 2003. Foreign catches (including discards) from 1979 onwards were available from the Scotia–Fundy and Newfoundland Observer Programs (SFOP and NFOP, respectively). Landings data for the Northwest Atlantic (not including Japanese vessels) are from ICCAT statistics for area 92 (ICCAT 2005), and those for Japanese vessels were derived from FAO statistics of the nominal catch of unspecified sharks and rays (and thus were not restricted to blue sharks) (FAO 2001). North Atlantic landings are derived from ICCAT statistics for the Atlantic shark stock (ICCAT 2005).

Calculation of unobserved bycatch

To estimate the magnitude of unobserved blue shark bycatch in the various large pelagic fisheries, bycatch was estimated by country, fishery, quarter, and year from SFOP observations made between 1986 and 2000, with bycatch defined as the summed weight of the kept and discarded blue sharks relative to the summed large pelagic catch (tuna, swordfish, and porbeagle). The summed large pelagic catch accounted for virtually all of the catch, and its use in the estimation avoided problems associated with the species sought being unknown. The analysis was restricted to Canadian, Japanese, and Faroese vessels, as they accounted for more than 99% of the blue shark catch. Full details on the

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estimation protocol are presented in Campana et al. (2002*a*, 2004).

Hooking mortality

A confounding issue in the interpretation of blue shark bycatch concerns the survival or mortality of the discarded sharks. In principle, after 1994, sharks discarded alive and in good health should not be included in any calculations of fishing mortality or nominal catch. However, many pelagic shark species suffer a high hooking mortality because of their requirement for continued swimming to move water over their gills to breathe. Unfortunately, there do not appear to be any published studies of hooking (discarding) mortality in sharks.

There is no objective method for determining what percentage of the injured, discarded sharks would subsequently die. However, detailed postcapture examinations of 111 commercially caught, injured sharks indicate that most were gut-hooked. Gut-hooked sharks would appear to be at the highest risk of death because of the potential for damage of internal organs and interference with feeding and (or) digestion; therefore we arbitrarily assumed a 50% mortality rate for gut-hooked sharks.

Commercial catch rate

Calculations of commercial catch rate (ln-transformed kilograms per hook) used as an index of abundance were based on directed longline catches for large pelagic species, which account for most of the blue sharks caught in Canada. All data came from the SFOP and are thus considered accurate. Initial examination of the catch rate data indicated that the major data sources could be categorized by country (Japan, Canada), area fished (around Newfoundland, eastern Scotian Shelf (NAFO division 4VW), and the southern region (NAFO division 4X, Georges Bank)), season, and species sought (bigeye tuna (*Thunnus obesus*), swordfish (*Xiphias gladius*), and bluefin tuna (*Thunnus thynnus*)). Catch rate trends in the southern region tended to be quite different (and based on a much smaller sample size) than those off Newfoundland and the Scotian Shelf, so only the latter two regions were used. Before the introduction of the ban on finning in 1994, discarded sharks were not necessarily counted by SFOP; therefore, the final catch rate analysis was restricted to the period after 1994.

Estimation of catch from the recreational fishery

The Canadian recreational shark fishery is designated as catch and release only (with the exception of shark derbies). Logbook returns from this fishery were low in number, providing little information on the magnitude of the total recreational catch. Therefore, we estimated the total recreational shark catch using a phone survey, then estimated catch mortality using an assumed hooking mortality rate.

A total of 1400–1800 recreational shark fishing licences were issued annually between 2001 and 2002. Of these, 201 recreational shark fishers were selected for over-the-phone interviews conducted between September and December 2002. A sample of 100 fishers was randomly selected and then contacted from the list of licences that were issued in 2002. Using the shark derby logs from the previous six years, an additional 100 "frequent" shark fishers were identified based on names that appeared more than once in the logs. These samples sizes represent ~10% of the licensees. Considerable effort was expended in contacting fishers who could not be contacted on first attempts, resulting in 162 successful interviews. Details of the survey and its results are presented in Campana et al. (2004).

Total annual recreational catch (excluding derbies) was estimated based on the percentage of active fishers, the mean annual catch from the shark fishing logs, and the mean weight of blue sharks in the population. The mean weight of an individual shark in the recreational shark catch (29 kg) was based on charter catches, which include undersized sharks not landed at derbies. The recreational shark fishery was assumed to catch 0.66 of the derby catch for the years before 2001, based on the observed catch proportion in 2001–2002.

Catch rates from shark tournaments

Estimation of catch rates at shark tournaments should provide an index of shark abundance. However, estimation is complicated by the presence of multiple fishers per boat, discarding of undersized sharks, and difficulties in assigning catches to specific fishers on the boat. Therefore an index based on the percentage of fishers successful in catching a shark at each derby was used. The resulting general linear model (GLM) was based on the overall fishing success at the five shark fishing derbies carried out annually since 1998.

Results

Migration from tagging studies

The migration pattern of blue sharks in Canadian waters was analyzed on the basis of tag recaptures from two sets of tagging studies. Most of the 2017 tags applied in the Canadian tagging study were applied before 1972, which makes this study most applicable to the early years of the longline fishery. With only 17 recaptures from this study, it was difficult to draw many conclusions. However, it was clear that at least some of the sharks migrated freely between inshore and offshore waters and between Canadian and US waters.

Most of the tagging effort in the NMFS program took place after 1990, thus providing a view of recent migration patterns. The NMFS program resulted in 188 recaptures in Canadian waters between 1974 and 2002: 171 from foreign tagging and 17 from Canadian tagging. Most of the tagged sharks recaptured in Canadian waters were tagged in the US, a pattern which would be expected given that most of the tagging effort was concentrated in the US (Fig. 1*b*). In contrast, most of the tags applied in Canadian waters were later recaptured in the central and eastern Atlantic, as far away as Africa (Fig. 1*a*). There was no obvious difference in migration pattern between males and females or between small and large sharks.

Commercial landings

Blue shark landings and (or) nominal catch in the Canadian Atlantic (NAFO areas 2–5) are known only for Canadian vessels landing their catch or for foreign vessels operating under 100% observer coverage within Canada's 200-mile limit. Landings peaked at around 250 t in 1994, declining thereafter to only 19 t in 2003 (Table 1). Only Canadian, Japanese, and Faroese vessels are known to have caught

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Fig. 1. Blue sharks (*Prionace glauca*) (*a*) tagged or (*b*) recaptured between 1971 and 2002 in Canadian waters under the US National Marine Fisheries Service tagging program. Bathymetric contour is 200 m.

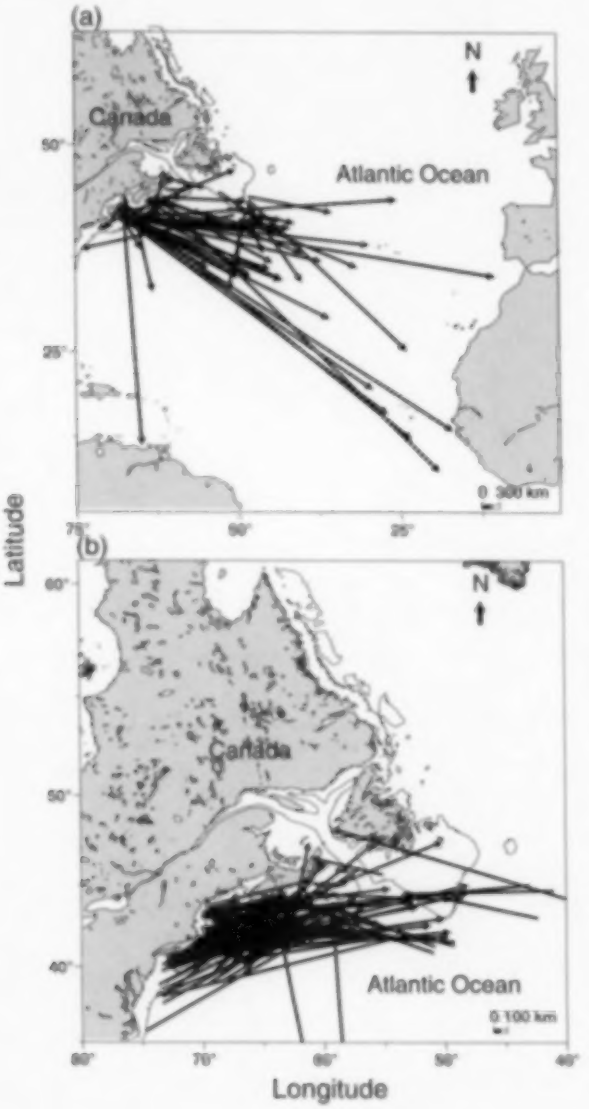
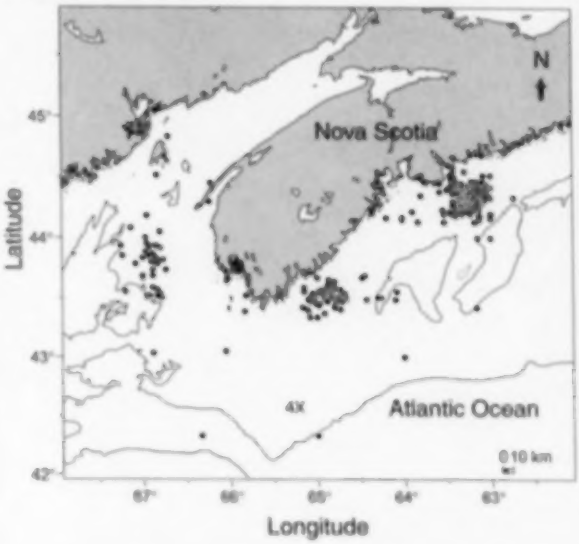


Fig. 2. Random subsample of fishing location of sharks caught at shark fishing tournaments off of Nova Scotia (1996–2002). Bathymetric contour is 200 m.



significant quantities of blue shark in Canadian waters. In the Northwest Atlantic as a whole (north of Florida), mean reported catches are somewhat larger, averaging 200–500 t in the 1990s. North Atlantic nominal catches are substantially larger, averaging over 30 000 t since 1998. However, much of this reported catch is believed to have been caught in the Northeast Atlantic.

Blue shark landings by Canadian vessels are very small, averaging 52 t·year^{-1} since 1990. Most of the landings are from longlines, although recreational shark fishing derbies averaging 10–20 t annually have accounted for a growing proportion of the landings in recent years. Most of the commercial catch is restricted to the Scotian Shelf in the first half of the year, extending northwards into the Gulf of St. Lawrence and the Newfoundland shelf between July and December.

Catch from shark tournaments (derbies)

The weight of sharks landed at recreational shark tournaments has increased from around 4 t in 1993 (the first year of the derbies) to around 15 t in recent years (Table 2). Although shortfin mako (*Isurus oxyrinchus*), thresher (*Alopias vulpinus*), and porbeagle (*Lamna nasus*) sharks have all been caught at derbies, blue sharks accounted for 99% of all landings.

Shark derbies in Atlantic Canada are all currently located in Nova Scotia. On average, there have been 5–6 derbies held each year between late July and mid-September. Fishing effort and catch at each derby is detailed in Campana et al. (2004). Fishing locations are centred in the waters around Halifax and Lockeport and in the southern Bay of Fundy (Fig. 2).

Catch from the recreational shark fishery

The percentage of recreational shark licensees who actually fished for sharks in 2001 or 2002 was relatively small: 7% of the random sample and 14%–22% of the "frequent" fishers. Of these, most fished two to three times per year, catching 4–12 sharks annually. The median annual catch per licence was 0.5 sharks in 2001 and 0.9 sharks in 2002. There was no evidence that frequent fishers were any more successful than the random sample of fishers.

Less than 2% of the recreational licensees returned fishing logs at the end of the fishing year. The average number of trips per year was very similar to that reported in the phone survey. However, the mean number of sharks caught per year

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Table 1. Reported blue shark (*Prionace glauca*) landings (tonnes) by country.

	Canadian Atlantic (NAFO areas 2–5)					Northwest Atlantic					
Year	Canada	Faroe Islands	Japan	Other	Total	Japan	USA	Other	Unspecified pelagic sharks	Total	North Atlantic
1979			4		4					4	
1980				13	13					13	4
1981			1		1					1	12
1982			2		2					2	9
1983			1		1					1	8
1984					0					0	14
1985					0					0	39
1986			13		13		1			14	51
1987			38		38		360			398	593
1988			5		5		241			246	512
1989			10		10		232			242	561
1990	8		13		21	140	394			555	2 261
1991	31	16	5		52	198	375			625	3 217
1992	101	30	30		161	345				506	2 045
1993	24	44	47		115	553	17			685	7 208
1994	138		116		254	450	1		4	705	8 196
1995	152		73		225	397	347	3		972	8 403
1996	23		173		196	238	169	1	160	604	8 398
1997	19		36		55	99	89	1	6	244	35 951
1998	14		17		31	115	3	1		150	34 298
1999	67		11		78	170	2	9	31	259	34 722
2000	34		0		34	83				117	32 297
2001	8		0		8	116				124	29 942
2002	25		0		25					25	29 583
2003	19		0		19					19	

Table 2. Species of shark landed at shark derbies between 1993 and 2003.

	Blue shark		Mako		Porbeagle		Thresher shark		Total	
Year	No.	Weight	No.	Weight	No.	Weight	No.	Weight	No.	Weight
1993	93	3 636	0	0	1	10	0	0	94	3 646
1994	117	5 048	0	0	0	0	0	0	117	5 048
1995	122	6 464	0	0	0	0	0	0	122	6 464
1996	114	4 967	1	46	0	0	0	0	115	5 013
1997	273	10 315	0	0	0	0	0	0	273	10 315
1998	269	10 406	0	0	0	0	0	0	269	10 406
1999	300	14 598	0	0	0	0	0	0	300	14 598
2000	235	15 488	3	489	0	0	0	0	238	15 977
2001	162	7 594	0	0	1	57	1	84	164	7 735
2002	327	19 324	4	674	1	27	0	0	332	20 026
2003	342	12 017	3	399	1	132	0	0	346	12 548

Note: Weights are live equivalent weights (kg). Blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), porbeagle (*Lamna nasus*), thresher (*Alopias vulpinus*).

(2.4) was much less than that reported in the phone survey. Because the recreational fishing logs were returned voluntarily and prepared after more thought than the phone surveys, we assumed that their report of average catch was more accurate than those of the phone surveys. Charter fishery catches averaged 162 sharks annually spread across 32 trips.

Based on a 7% participation rate and the mean annual catch from fishing logs (with the charter fishery being treated separately), a total of 431 sharks weighing about 12.5 t were caught annually in the non-derby recreational shark fishery.

Observed commercial bycatch

The SFOP has maintained 100% coverage of foreign fisheries in the Canadian zone since 1987, thus allowing accurate determinations of both nominal catch and bycatch. SFOP coverage of domestic longline vessels has been considerably less, probably on the order of 5%. Nevertheless, SFOP ob-

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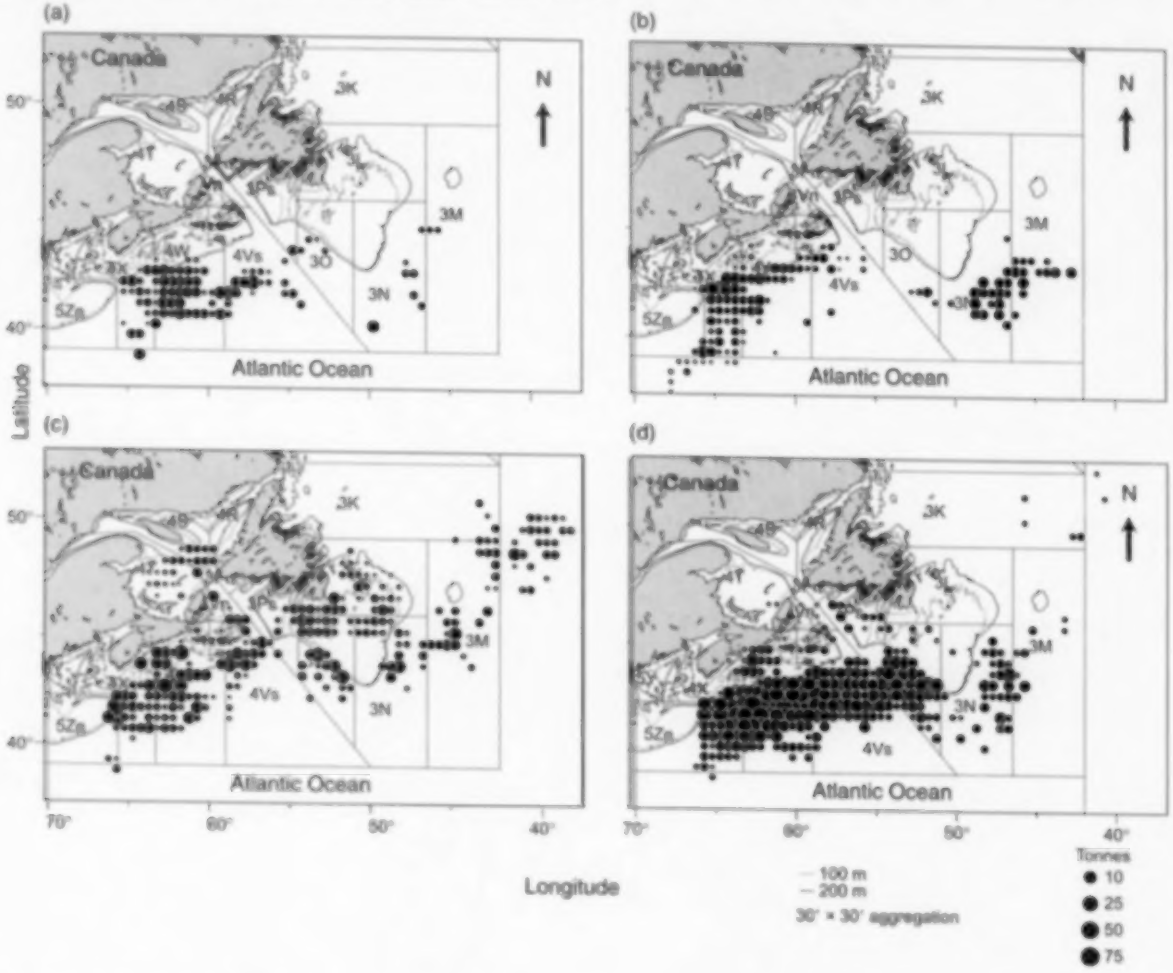
Fig. 3. Blue shark (*Prionace glauca*) catch location by season as observed by the Scotia–Fundy Observer Program on Canadian, Japanese, and Faroese vessels fishing swordfish (*Xiphias gladius*), tuna (*Thunnus* spp.), or porbeagle sharks (*Lamna nasus*) between 1986 and 2004: (*a*) January–March; (*b*) April–June; (*c*) July–September; and (*d*) October–December. North Atlantic Fisheries Organization (NAFO) division boundaries are shown. Bathymetric contour is 200 m.



servations indicate that Canadian, Japanese, and (in earlier years) Faroese longliners caught substantially larger numbers of blue sharks than would otherwise be known from nominal catch statistics. Observed catch and bycatch between 1990 and 1999 averaged about 250 t annually, with most of that coming from Japanese vessels. In most years, virtually all of the blue shark catch was discarded. Since 1999, virtually all observed catch and bycatch has been by Canadian vessels. Observed catch locations mapped by quarter over the period 1986–2004 indicate that most of the Canadian and Japanese bycatch occurred in deep waters off the continental shelves of Nova Scotia and Newfoundland, increasing in quantity through the year (Fig. 3). Significant catches have also been observed in the deep basins of the Scotian Shelf. Catch locations of Japanese longliners occurred almost exclusively off the continental shelf, primarily in the first and last quarters of the year, in part because of regulations restricting the area and time of the fishery. The location of blue shark bycatch in the Canadian and Faroese porbeagle fishery was somewhat different, being more localized on the Scotian and Newfoundland shelves, as well as in the Gulf of St. Lawrence.

Unobserved blue shark bycatch estimates

For the six large pelagic fisheries (albacore, yellowfin, and bigeye for both Canada and Japan) other than porbeagle, mean blue shark bycatch accounted for 26%–152% of the total large pelagic catch, with an overall mean of 34% (n = 5787 sets). Bycatch proportions in individual sets often exceeded 100%. Annual bycatch estimates averaged less than 100 t for the bluefin tuna fishery, less than 500 t for other tuna, and around 2000 t for the swordfish fishery. Blue shark bycatch in the porbeagle fishery was substantially less, averaging 7% for an annual bycatch of about 50 t.

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Table 3. Estimates of blue shark (*Prionace glauca*) hooking mortality in the commercial and recreational fisheries.

Year	Fishery	*n*	Percent healthy	Percent injured[a]	Percent dead[b]
Scientific study on commercial vessel (Sept. 2003)					
2003	Blue shark	105	38	44	18
Scotia–Fundy Observer Program					
2001	Swordfish	2035	78	5	17
	Tuna	2606	82	12	6
2002	Swordfish	2219	25	64	11
	Tuna	4265	75	18	7
2003	Swordfish	980	88	1	11
	Tuna	1518	83	10	7
	Porbeagle	116	59	16	23
Mean			70	18	12
Recreational fishery (Aug.–Oct. 2002)					
2002	Blue shark	111	63	37	0

[a]For 2002 and 2003 blue shark fishery, fish were gut-hooked, but observers were unable to tell if it was a fatal injury.
[b]For 2002 blue shark fishery, 9% were in poor condition upon release and presumably would have died.

Hooking mortality

Three sets of studies were made on blue sharks caught as part of both commercial and recreational shark fisheries (Table 3). The percentage of blue sharks that were dead upon retrieval was similar in both the scientific and observer studies: 10%–20%. These values are also consistent with the mortality values of 13.5% and 20% reported by Francis et al. (2000, 2001) for blue sharks caught in the New Zealand pelagic longline fishery. Because mortality is at least in part associated with the amount of time spent on the hook, the absence of dead sharks in the recreational fishery is understandable.

Based on the results of the scientific study and assuming a 50% mortality rate for injured (gut-hooked) sharks, 60% of the discarded sharks would be expected to survive capture in the commercial fishery. Survival in the recreational fishery would be expected to be higher at 81%. Many of the gut-hooked sharks looked healthy from the outside, which may explain the large variations in the percentages of healthy and injured sharks between the scientific and observer studies (Table 3). Because most discards were finned before June 1994, those discards were assumed to be 100% dead.

Total catch mortality

Total estimated annual blue shark catches and discards in Canadian waters are shown (Table 4). Discards from the Canadian large pelagic fisheries were responsible for the largest proportion of blue sharks caught in Canadian waters since 1986. However, total estimated catch mortalities, based on the discard rates and hooking mortalities presented earlier, are lower, averaging around 1000 t·year^{-1} over the time series (Table 4; Fig. 4). The proportion of catch mortality contributed by fishing at derbies was negligible, averaging 3% of the total catch mortality in recent years.

Length composition

Measurements by scientific staff at shark derbies since 1993 highlight a striking difference between the length compositions of the males and females: mature females were virtually absent from the derby catches, whereas mature males were caught more frequently than immature males (Fig. 5). Immature females were the category most represented in the catch.

To determine if the length composition in the derby catches was representative of the population sampled by the commercial fishery, a series of paired comparisons were made between the derby length frequencies and those from the commercial fishery (as measured by observers), matched for year, season, and area. In all cases, the presence of small sharks (<140 cm) seen in the commercial fishery was not well represented in the derby catches. The absence of small sharks in the derby catches was almost certainly the result of regulations, which specify a 6-foot (183 cm total length) minimum size limit. In addition, although the length frequencies of the females were similar between commercial and derby catches, large males (>200 cm) were overrepresented in the derbies. This overrepresentation is likely due both to specific targeting of large males by derby participants and by size-selective hooking of smaller sharks by commercial fishing gear. There may also have been some understandable reluctance by observers on board commercial fishing vessels to measure very large, live sharks.

Analysis of the size composition of the recreational charter fishery indicated that it was similar to that of the derbies, but with the addition of large numbers of sharks below 140 cm. Such a size composition is more consistent with that of the commercial fishery, supporting the view that the derbies and commercial fishery are actually sampling the same population but that selectivity has distorted the derby catch composition.

Catch rates

The overall trend in catch rate (used as a proxy for relative abundance) was analyzed at the set-by-set level using a GLM with year, region, season, species sought, and vessel identity (CFV) as factors. Models with CFV tended to outperform models using country (but not CFV) as a factor, but vessels fishing only a single year confounded the interpretation of the analysis. Therefore, only vessels that fished at least 10 sets in at least two years were included. Because of data availability, the analysis was restricted to the Newfoundland and Scotian Shelf regions in the fall and winter for the period after 1994. GLM trends for swordfish and bigeye tuna were similar and therefore were left together in the same analysis; the different trend for bluefin tuna necessitated a separate analysis, and because it was less informative, it was not presented here (Campana et al. 2004).

The GLM of blue shark catch rate based on the bigeye tuna and swordfish data indicated that all factors but season and species sought were significant (Table 5). The marginal catch rate based on the significant factors indicated that catch rates have declined significantly by 53% (6.6% per year) since 1995 (Fig. 6). Although this GLM used most of the data, there was some aliasing between the early Japanese and later Canadian data. Nevertheless, when the model was

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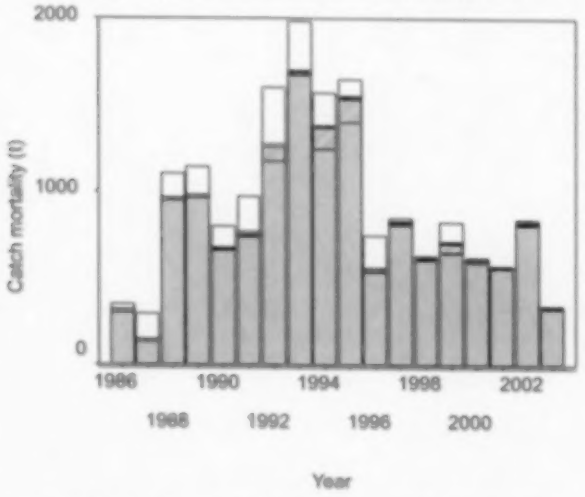
Table 4. Total blue shark (*Prionace glauca*) catch (tonnes) in Atlantic Canada by source.

Year	Derbies	Recreational[a]	Landed commercial[b]	Observed foreign catch[c]	Observed foreign discards[d]	Observed Canadian discards[e]	Estimated catch and discards from Canadian fishery[f]	Total estimated catch mortality[g]
1986				13	32		801	365
1987				38	123		367	308
1988				6	146		2421	1120
1989				10	172	42	2446	1160
1990			8	13	125	7	1680	818
1991			31	11	207	20	1857	992
1992			101	60	285	2	2940	1622
1993	4	3	21	91	205	14	4190	1998
1994	5	3	133	116	210	53	3118	1586
1995	6	4	145	73	100	106	3505	1667
1996	5	3	18	173	61	37	1352	762
1997	10	7	9	36	0	28	2026	867
1998	10	7	4	17	17	210	1518	646
1999	15	10	53	11	282	185	1616	840
2000	15	11	19	0	3	70	1471	626
2001	8	13	0.4	0	0	179	1426	581
2002	19	13	5	0	4	228	2029	840
2003	12	13	6	0	0	85	811	345

[a]Catch and release fishery, excluding derbies; 2001–2003 estimated from recreational logbooks and phone survey; other years assumed to be 0.66 of derby catches based on tag recaptures and 2002–2003 ratios.
[b]Canadian landings only.
[c]Scotia–Fundy Observer Program measurements of all foreign-kept catch.
[d]Scotia–Fundy Observer Program measurements of all foreign-discarded catch.
[e]Scotia–Fundy Observer Program measurements of Canadian discards; coverage was about 5% of fleet.
[f]Sum of bycatches from porbeagle, bluefin tuna, swordfish, and other tuna fisheries.
[g]Sum of landed catches and hooking mortality applied to recreational, domestic commercial, and foreign discards; foreign discards before 1994 assumed to be dead as the result of finning.

Fig. 4. Total catch mortality (tonnes (t)) by source for blue sharks (*Prionace glauca*) caught in Atlantic Canadian waters: Canadian landings, hatched bars; tournament catches, solid bars; foreign catches, open bars; Canadian discards, shaded bars.



rerun using Canadian vessels only, the predicted trend was very similar to that presented in Fig. 6.

Additional models were run to assess the sensitivity of the results. Models using all vessels (rather than vessels fishing multiple years) produced marginally higher correlation coefficients but with fewer estimable years. Predicted trends were similar. In contrast, models using country rather than CFV explained much less of the variation. Therefore, the model presented in Table 5 was selected as the best available.

Fishing success at shark fishing tournaments suggested a significant decline of 27% (5.4% per year) in catch rates since 1998 (Fig. 7). A standardized catch rate prepared using a binomial dependent variable (successful/unsuccessful) and derby location as a fixed factor in a GLM was not statistically significant. Because individual catch rates were not available, an index based on the percentage of fishers successful in catching a shark at each derby was used. This model was less than ideal as the derbies represented fixed factors and thus year × derby interaction terms could not be assessed. Nevertheless, when scaled to the same scale as the standardized commercial catch rate model, the trend across years was similar. These results suggest that the derbies and the offshore commercial fishery are samples from the same population and that the catch rate in recent years has been less than that of earlier years.

Exploitation rate from tag recaptures

The exploitation rate of blue sharks in Canadian waters was estimated through Petersen analysis of tag recaptures (Ricker 1975). Despite the relatively high tagging effort in the Canadian study, there were only 17 recaptures in the 1960s and 1970s. Annual exploitation rates never exceeded

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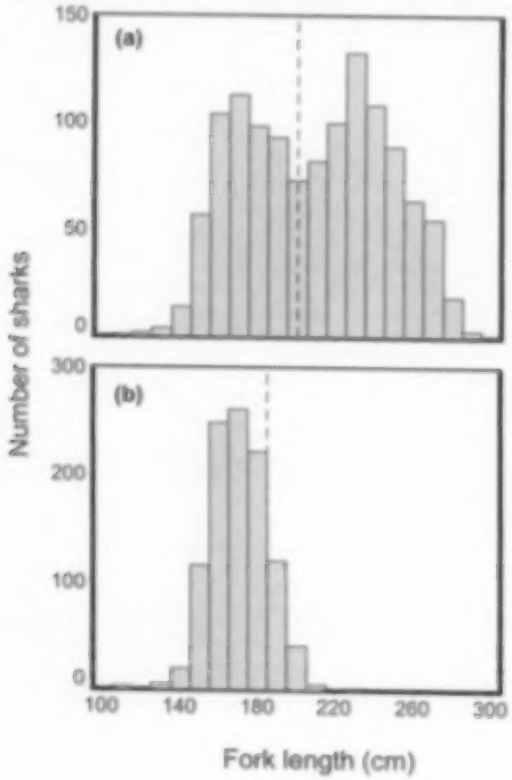

Fig. 5. Length frequency by sex for blue sharks (*Prionace glauca*) examined at shark fishing tournaments. Length at 50% maturity for each sex is shown by the broken vertical lines. (*a*) The mean fork length of males was 208 cm (n = 1213); (*b*) the mean fork length of females was 170 cm (n = 1047).

1%, and overall recapture rates (which will always overestimate exploitation rate) never exceeded 1.6% (mean of 0.4%). Although the tag-reporting rate for blue sharks was undoubtedly lower than that of more commercially valuable species, we suspect that the low recapture rate was due in part to the relatively low longline fishing effort of the period, as well as emigration out of the area.

Analysis of the US tagging data provided several relative indices of exploitation rate in Canada. Mean exploitation rate in the tagging year, weighted by tagging effort, was 0.78% between 1992 and 2002, corresponding to a mean annual observed catch of 321 t. Nonreporting of tags by the commercial fishery would result in this calculated exploitation rate being an underestimate.

To provide an estimate of exploitation rate which is unaffected by reporting rate, we repeated the calculation using a subset of the fishery — the recreational fishery — which is highly motivated to report any recovered tags. Because the recreational fishery is responsible for most of the recent tagging effort on blue sharks, it is safe to assume that the tag-reporting rate is close to 100% in this segment of the fishery. To calculate the recreational exploitation rate, we looked only at Canadian tags applied inshore in known recreational shark fishing grounds (and therefore assumed to represent tags applied by recreational fishers) (n = 212) and recaptured inshore during shark fishing derbies in the same year (n = 1), multiplied by 2 to allow for the fact that tags were applied throughout the recapture season. Mean weighted exploitation rate by the recreational fishery at scientifically monitored fishing tournaments was very small (0.94%). However, the confidence interval around the estimate was broad, ranging from 0.1% to 7%. The fact that the tagging area did not represent a closed population implies that exploitation rate would be underestimated, although it is likely that within-season emigration out of the area was low.

As an overall comparison of recent and historic blue shark exploitation rate, we compared the overall recaptures per tag in the period 1961–1972 with that of 1992–2002. The mean recapture rate increased from 0.009 to 0.089. Assuming comparable reporting rates in the two periods, this comparison suggests that fishing mortality on blue sharks increased 10-fold between the two periods. Longline fishing effort in the North Atlantic increased 8-fold between these two time periods (ICCAT 2005), which appears to explain much of the increased fishing mortality.

Trends in length composition

A biological indicator of increased exploitation rate is a long-term decline in length in the catch. There has been a significant decline in mean blue shark length in the observed longline catch since the late 1980s ($P < 0.05$; Fig. 8). Significant differences were also observed in the length composition between the Canadian and Japanese fleets ($P < 0.05$), but these are almost certainly due to differences in depths fished (Campana et al. 2002*a*). An index based on measurements made at the shark tournaments could not be used as the tournament length composition was not representative of the population.

Discussion

Our results indicate that the blue shark is the most frequently caught large shark in the Canadian Atlantic, despite negligible landings. The reported catch of blue sharks grossly underestimates both the actual catch (sum of landed catch and discards) and the catch mortality. The nominal catch of blue sharks by both domestic and foreign longline fisheries only accounts for about 5% of their actual catch. Based on reasonable estimates of bycatch mortality, the sum of nominal catch and bycatch mortality has averaged about 1000 t annually since 1986, with most of this being the result of discard mortality. This figure is larger than the annual average catch of porbeagle shark (*Lamna nasus*), for which there is a directed fishery (Campana et al. 2002*b*). The only shark species on the east coast of Canada that might be caught in larger numbers is the spiny dogfish (*Squalus acanthias*) (Rago et al. 1998).

Some members of the public have expressed concern that recreational shark fishing tournaments have had an adverse effect on the blue shark population. The weight of sharks landed at recreational shark tournaments has increased from around 4 t in 1993 to around 15 t in recent years. Blue sharks accounted for 99% of all sharks landed. The recreational catch-and-release fishery caught about another 13 t annually. However, these catch figures are very small com-

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Table 5. Results of the catch rate standardization model relating the catch rate (ln-transformed kilograms per hook) of blue shark (*Prionace glauca*) in bigeye tuna (*Thunnus obesus*) and swordfish (*Xiphias gladius*) fisheries to region, season, vessel (CFV), species sought (SPECS), and year (YR).

Source	Type III sum of squares	df	Mean square	*F*	Significance (*p*)
Corrected model	286.034	62	4.613	6.741	0.000
Intercept	5.832	1	5.832	8.521	0.004
CFV	86.729	12	7.227	10.560	0.000
YR	39.565	7	5.652	8.258	0.000
CFV × YR	4.097	8	0.512	0.748	0.649
SEASON	0.011	1	0.011	0.017	0.898
REGION	2.737	1	2.737	3.999	0.046
CFV × SEASON	2.508	3	0.836	1.222	0.301
CFV × REGION	2.180	5	0.436	0.637	0.672
YR × SEASON	0.373	2	0.186	0.272	0.762
YR × REGION	7.204	4	1.801	2.631	0.034
SEASON × REGION	0.513	1	0.513	0.749	0.387
SPECS	0.259	1	0.259	0.379	0.539
CFV × SPECS	0.069	2	0.035	0.051	0.951
YR × SPECS	0.000	0			
SEASON × SPECS	0.000	0			
REGION × SPECS	0.000	0			
Error	275.135	402	0.684		
Total	996.625	465			
Corrected total	561.169	464			

Note: $R^2 = 0.51$ (adjusted $R^2 = 0.43$).

Fig. 6. Standardized commercial catch rate (ln-transformed kilograms per hook ± 95% confidence interval) of blue shark (*Prionace glauca*) in Canadian and Japanese large pelagic fisheries targeting bigeye tuna (*Thunnus obesus*) and swordfish (*Xiphias gladius*).

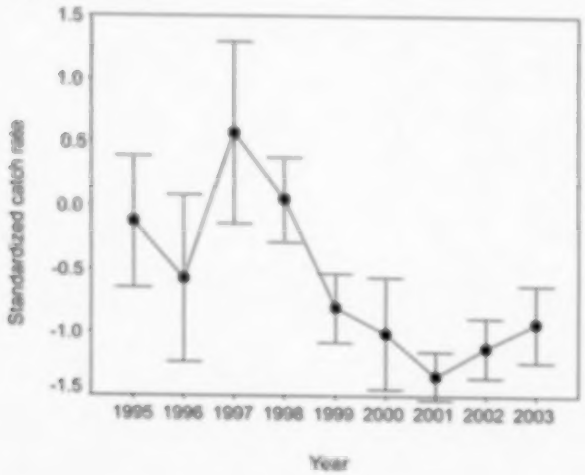
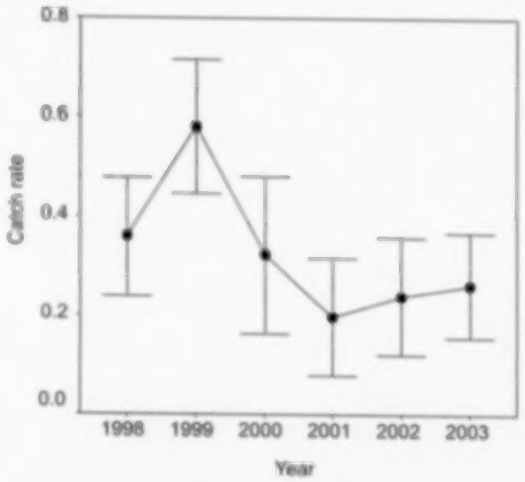


Fig. 7. Catch rate (sharks per fisher ± 95% confidence interval) of blue sharks (*Prionace glauca*) at recreational shark fishing tournaments.



pared with overall catch mortality in Canadian waters, accounting for about 3% of the total fishing mortality. Thus tournaments have had a negligible effect on population abundance and overall mortality. The ethical questions surrounding shark tournaments (which are essentially trophy tournaments) were not addressed by this analysis.

Two indices of population abundance suggest that blue shark abundance in the Canadian Atlantic has declined in the past decade. Standardized catch rate indices from both the commercial large pelagic fishery and recreational shark tournaments suggest a decline in blue shark abundance of about 5%–6%·year^{-1} since 1995. Similarly, the median size of blue sharks in the commercial catch has declined since 1987, suggesting an increase in mortality rate. In the only published

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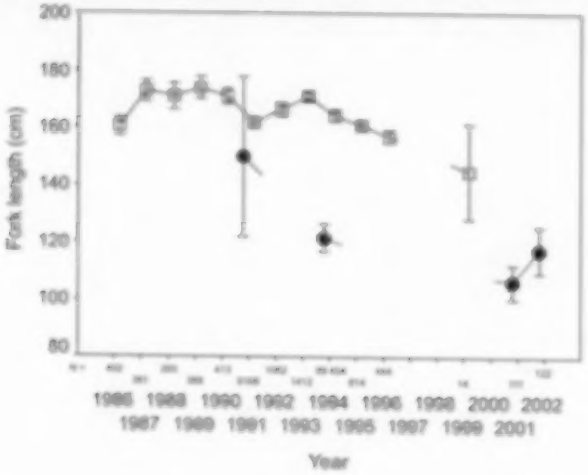
Fig. 8. Trend in mean fork length (±95% confidence interval) of blue sharks (*Prionace glauca*) caught in fall and winter in Japanese (□) and Canadian (●) pelagic longline fisheries.



overview of the status of Northwest Atlantic blue sharks, Baum et al. (2003) used a model of commercial catch rate from the logbooks of US fishers to conclude that the population had declined monotonically by 60% (4.3%·year^{-1}) over the period 1986–2000. However, this conclusion was at odds with the 9.6% decline, characterized by increasing and then decreasing abundance, for the area of highest blue shark abundance off of eastern Canada. Although Baum et al. (2003) acknowledged that the Atlantic Canada trend did not match the modelled overall trend, it is difficult to rationalize the very different trends between the overall model and the region with the greatest number of blue sharks. It is unlikely that the unregulated fishers' logbooks used by Baum (2002) and Baum et al. (2003) were as accurate as the observer records reported here. Nevertheless, their analysis covered a broader proportion of the blue shark geographic range than was represented in the Canadian data presented here. Therefore, it is interesting to note that the observed (as opposed to the modelled) Atlantic Canada time series of Baum (2002) was very similar to the GLM fit to the Canadian and Japanese observer time series of Fig. 7. Based on this correspondence and assuming that catch rate reflected relative abundance in the same way across the time series, it seems likely that the relative abundance of blue sharks has declined since the 1990s.

A perspective on the status of North Atlantic blue sharks

It is unlikely that the reported catch of blue shark in the North Atlantic is anywhere near the true catch: with a negligible commercial value, most blue sharks are discarded at sea with no record of having being caught. This point was highlighted in the Canadian Atlantic, where both the domestic and the foreign nominal catch grossly underestimated the catch mortality, let alone the catch.

Given reliable large pelagic catch records in the North Atlantic — the catch of valuable tuna and swordfish species is monitored closely by ICCAT — it should be possible to approximate the catch of blue shark in the large pelagic fisheries by applying a bycatch proportion calculated from observed fisheries. Blue shark bycatches by both foreign and domestic fisheries have been observed and recorded for 17 years in the Canadian Atlantic; therefore, the proportion of blue shark in the large pelagic catch is well known. A major assumption of this approach is that the proportion of blue shark in the large pelagic catch of the observed fishery is similar to that elsewhere in the North Atlantic. Campana et al. (2004) reviewed the literature for estimates of blue shark catch rate throughout the North Atlantic and reported that the overall blue shark catch rate (mean ± 95% confidence interval) was 18.4 ± 8.3 blue sharks per 1000 hooks. Although differences among studies were noted, there were no consistent differences in blue shark catch rate between eastern and western Atlantic, or between Canadian, American, and European fisheries. More importantly, the ratio of blue shark to the directed species appeared to be similar across locations. Thus, as a first approximation, it appeared reasonable to assume that relative blue shark abundance was similar in all North Atlantic large pelagic fisheries.

The total catch of large pelagics documented by ICCAT for the Atlantic in the year 2000 was 620 808 t (from ICCAT Task 1 online database, available at http://www.iccat.es/data/taski_excel.zip). To restrict the estimate to the North Atlantic, we excluded all catch entries from the South Atlantic and reduced by 75% the entries from the eastern and western tropics (assuming that one-half of the tropics was from the northern tropics and that blue shark abundance was less in tropical waters than in temperate waters). The final North Atlantic large pelagic catch estimate for 2000 was 316 182 t, which is likely to be a conservative estimate. Assuming a 34% bycatch of blue sharks (as calculated earlier), the total blue shark catch is estimated at more than 100 000 t. This value is almost four times the nominal catch listed in Table 1. Assuming a 40% hooking mortality in the longline fishery and an arbitrary 20% mortality in the purse seine fishery (as hook injury would not be a source of mortality in purse seines), the catch mortality of blue sharks in the year 2000 was estimated to be about 37 000 t. This value is considerably more than the nominal catch but is still likely to be an underestimate because of nonreported large pelagic catch and the fact that the large pelagic catch rate is somewhat higher in the Canadian Atlantic than elsewhere (a high large pelagic catch rate would result in a lower blue shark to large pelagic catch ratio). In addition, our estimate of blue shark catch mortality does not take into account any mortalities resulting from finning in unregulated, unobserved international waters.

An independent estimate of North Atlantic blue shark catch mortality is possible using the exploitation rate calculated from tagging and a previously reported fishing mortality estimated from the catch curve analysis of Campana et al. (2004). The Canadian exploitation rate from the US tagging study was 0.0078, corresponding to an observed catch in Canadian waters of 321 t. Given the population-level F of 0.66 (= exploitation rate of 0.48) from the fast-growth catch curve (Campana et al. 2004, their fig. 22) and assuming a 75% tag-reporting rate from the observed catch, the North Atlantic catch mortality would be 26 300 t.

These two independent approximations of total North Atlantic blue shark catch mortality, based on bycatch ratios and

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mortality estimates, suggest North Atlantic catches of more than 100 000 t and catch mortalities of between 26 000 and 37 000 t. As first approximations, these probably provide conservative estimates of actual blue shark catch mortality in the North Atlantic, although they are in line with the blue shark catches estimated by ICCAT (2005). Nevertheless, the Petersen analysis of tag recaptures indicated that the exploitation rate in Canadian waters appears to be but a small portion of the total. Similarly, the total Canadian catch mortality was only about 2% of the total estimated catch mortality for the entire North Atlantic. Therefore, the Canadian contribution to overall population mortality appears to be very low.

An obvious question to ask is to what extent do indices of blue shark abundance and mortality in Canadian waters reflect those for elsewhere in the Atlantic. The tagging studies indicated that most of the tagged blue sharks recaptured in our waters were tagged in the US. In contrast, most of the tags applied in Canadian waters were later recaptured in the central and eastern Atlantic, some as far away as Africa. Overall, the tagging studies were consistent with the view that blue sharks are highly migratory, with no evidence of extended residency in Canadian waters. These results are consistent with those of previous tagging studies, which show high flux rates among areas (Casey and Kohler 1991), and suggest that Canadian indices of blue shark population status may be a reasonable proxy for blue sharks elsewhere in the Northwest Atlantic. Nevertheless, it is clear that blue sharks are not randomly mixed in the Atlantic Ocean as a whole. Mature females were rare in both the tournament and commercial catches, presumably because of their absence from Canadian waters. They also appear to be rare along the eastern coast of the US (Pratt 1979) but somewhat more common in the Northeast Atlantic (Buencuerpo et al. 1998). Thus the North Atlantic population as a whole appears to be a heterogeneous mixture by size and sex.

So how does the blue shark population manage to survive in the face of such high catch mortalities? A life table analysis using demographic values drawn from the literature and a value for the instantaneous rate of natural mortality (M) of 0.23 indicates that the intrinsic rate of population growth (r) in an unfished population would be about 0.36 (Campana et al. 2004). This translates into a 43% annual rate of increase in the absence of fishing. F_{MSY} (instantaneous rate of fishing mortality at maximum sustainable yield) would be about 0.18. Assuming 100% availability of females of all ages to the fishing gear, an instantaneous fishing mortality (F) of 0.32 would result in zero population growth. Such values of F are high by shark standards but are consistent with published views that blue sharks are relatively resilient to moderate fishing pressure and are both productive and resilient compared with other shark species (Cortés 1998; Smith et al. 1998; Frisk et al. 2001). This may explain why blue sharks have been slow to decline in the face of what appears to be a very high overall catch mortality. An additional factor aiding their persistence is the fact that few mature females are caught either in Canadian or American waters (Pratt 1979; this study).

Blue sharks have low commercial value and are discarded in great numbers by commercial pelagic fisheries. Despite their persistence to this point, their decline in relative abundance, decline in median size, and their high overall exploitation rate are all indicators of excessive mortality. The presence of a highly migratory population in the international waters of the North Atlantic complicates any attempt at concerted management or conservation. Nevertheless, continued and careful monitoring appears to be warranted.

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PERSPECTIVE / PERSPECTIVE

Information needs for assessing critical habitat of freshwater fish

Jordan S. Rosenfeld and Todd Hatfield

Abstract: The core assumptions of critical habitat designation are a positive relationship between habitat and population size and that a minimum habitat area is required to meet a recovery target. Effects of habitat on population limitation scale from (*i*) effects on performance of individuals (growth, survival, fecundity) within a life history stage, to (*ii*) limitation of populations by habitats associated with specific life history stages, and (*iii*) larger-scale habitat structure required for metapopulation persistence. The minimum subset of habitats required to achieve a recovery target will depend on the extent, quality, and spatial configuration of habitats available to sequential life history stages. Although populations may be limited by available habitat for a single life history stage, altering habitat quality for subsequent stages will also affect individual survival and population size, providing multiple leverage points within a life history for habitat management to achieve recovery targets. When habitat-explicit demographic data are lacking, consequences of uncertainty in critical habitat assessment need to be explicit, and research should focus on identifying habitats most likely to be limiting based on species biology.

Résumé : Les présuppositions fondamentales qui sous-tendent la désignation des habitats critiques sont l'existence d'une relation positive entre l'habitat et la taille de la population et la nécessité d'un habitat minimal afin de pouvoir atteindre un objectif de récupération. À différentes échelles, les effets de l'habitat sur la limitation des populations vont (*i*) d'effets sur la performance individuelle (croissance, survie, fécondité) pendant une étape particulière du cycle, à (*ii*) la limitation des populations par des habitats spécifiques à certaines étapes du cycle et finalement à (*iii*) la nécessité d'une structure d'habitat à plus grande échelle pour la persistance de la métapopulation. Le sous-ensemble minimal d'habitats requis pour atteindre un objectif de récupération va dépendre de l'étendue, de la qualité et de la configuration spatiale des habitats disponibles aux étapes successives du cycle. Bien que les populations puissent être limitées par la disponibilité d'habitats à une seule étape de leur cycle, une modification de la qualité de l'habitat pour les étapes subséquentes affectera aussi la survie individuelle et la taille de la population, ce qui fournit de multiples points d'intervention au cours d'un cycle biologique pour atteindre les objectifs de récupération par l'aménagement des habitats. Lorsqu'il n'existe pas de données démographiques spécifiques aux habitats, il faut que les conséquences de l'incertitude dans l'évaluation des habitats critiques soit explicite; la recherche devrait alors se concentrer sur l'identification des habitats qui sont les plus susceptibles d'être limitants d'après la biologie de l'espèce.

[Traduit par la Rédaction]

Introduction

Many developed nations, including Canada, have recently enacted legislation to prevent extinction of endangered species to fulfill domestic and international commitments (e.g., Rio Biodiversity Convention). Identification and protection of critical habitat is central to the management of species at risk. The rationale for protecting critical habitat is rooted in the observation that particular habitats are often disproportionately important to population limitation (Fausch et al. 2002), and therefore they represent priorities for habitat protection. The need to designate critical habitat is recognized by scientists, resource managers, and the general public, but operational definitions, approaches, and information requirements for identifying critical habitat remain poorly defined.

Credible designations of critical habitat are necessary for two reasons: first, designation of critical habitat based on inaccurate science may fail to ensure the long-term persistence of species at risk. Second, critical habitat designations that affect economic activity will be closely scrutinized by

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stakeholders who bear the lost opportunity costs of habitat protection and will be challenged if their scientific basis is questionable.

Defining critical habitat remains one of the most challenging problems of species management because it involves multiple aspects of population biology, ranging from local habitat effects on growth and survival of individuals to large-scale metapopulation and landscape issues. Despite its complexity, the core issue is the same for all species: to determine the role of habitat in population limitation and viability (by limitation we mean the influence of a factor on population size or carrying capacity, as opposed to regulation, which is a process whereby density-dependent effects maintain a population near the carrying capacity of a habitat). Because time and resources are rarely available to assess all aspects of the role that habitat plays in population limitation, biologists need to focus research efforts on habitats most likely to be limiting the species of interest. For species at risk, the challenge is to correctly identify and collect the minimum information required to credibly identify critical habitat in a short time frame and to refine these designations as future resources permit.

The primary objective of this review is to provide meaningful biological interpretations of critical habitat and a conceptual framework for prioritizing data collection in support of critical habitat designation. We first provide practical operational definitions of critical habitat. We then develop a conceptual framework for identifying the information needed for critical habitat assessment based on the roles habitat plays in population limitation. Finally, we illustrate application of the framework using selected case studies for species with divergent biologies and distributions representing a broad spectrum of information needs.

Legal and practical definitions of critical habitat

The fundamental premise of critical habitat protection is that certain habitats are more important than others for species persistence, and this hierarchy of importance should guide the prioritization of habitat protection. The legal definition of critical habitat in the US Endangered Species Act is

> …the specific areas within the geographical area occupied by the species…on which are found those physical or biological features essential to the conservation of the species. [Endangered Species Act of 1973]

The equivalent definition of critical habitat in the Canadian Species at Risk Act is

> …the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in a recovery strategy or in an action plan for the species. [Species at Risk Act 2002, s. 2(1)]

Both of these definitions are clear in intent but can be interpreted so broadly that they provide limited practical guidance for identifying critical habitat. This wording is presumably deliberate; rather than constrain designation through a restrictive legal definition, the identification of critical habitat is deferred to experts involved with species recovery. The onus is therefore placed on the recovery scientists to justify critical habitat designation using the best information available. Criteria for identification of critical habitat under the US Endangered Species Act specifically require consideration of social–economic impacts (U.S. General Accounting Office 2003). Under Canadian law, it appears that the intent is for the identification of critical habitat in the Recovery Strategy to be based purely on the biology of the species, but recovery activities identified in the Recovery Planning process (including the identification of critical habitat) are directed to consider social–economic impacts, and the ultimate discretion for accepting the definition of critical habitat recommended by recovery team scientists remains with the federal Minister of Environment. The federal Minister of Environment may choose to protect only a subset of habitats recommended by the recovery team or may choose to not list a species at all if the socio-economic impacts of recovery (e.g., protection of critical habitat) are deemed unacceptable (Irvine et al. 2005).

The Species at Risk Act also includes a definition of habitat that has broad implications for critical habitat designation. Habitat for aquatic species is defined as

> …spawning grounds and nursery, rearing, food supply, migration, and any other areas on which aquatic species depend *directly or indirectly* [our emphasis] in order to carry out their life processes, or areas where aquatic species formerly occurred and have the potential to be reintroduced… [Species at Risk Act 2002, s. 2(1)]

This definition provides for critical habitat to be defined both in terms of the abiotic (physical, chemical) and biotic (prey species, competitors, predators) features of the environment. It also explicitly permits the designation of presently unoccupied habitat, as well as habitat in which a species does not occur but whose loss or degradation will affect critical habitat directly used by a listed species. This latter circumstance is especially relevant to aquatic organisms, since aquatic habitats are subject to both indirect and cumulative impacts from diffuse (terrestrial) activities in a watershed (Schlosser 1991).

To complement these legal definitions of critical habitat, we suggest several practical working definitions that provide more general guidance and can serve as primary screening criteria for evaluating potential candidate critical habitat areas: (*i*) habitat that is disproportionately important whose singular or cumulative loss will result in significant population-level effects (for a recovered population); (*ii*) the minimum subset of habitats required for a species or population to persist (or achieve a recovery target); and (*iii*) habitats that are necessary to maintain ecosystem integrity and function.

The first working definition emphasizes the prioritization of habitat protection based on the population consequences of habitat loss or gain (i.e., if a particular type of habitat can be lost without population-level effects, then it is unlikely to be critical). The second definition emphasizes that the default objective may not be to protect the entire range of a species, and that for some species, different configurations or subsets of habitat of varying quality may ensure species persistence (although in other cases protection of all available habitat may be necessary).

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Fig. 1. Defining critical habitat is illustrated as a three step process. (1) A population recovery target is determined (N_{target}). (2) A relationship between habitat and abundance is developed. (3) The recovery target and the habitat–abundance relationship jointly define the quantity of habitat required to meet the recovery target (H_{crit}). H_{crit} will differ depending on the form of the habitat–abundance function. Habitat–abundance relationships will be linear if the number of recruits to a habitat increases proportionally with area (solid line). If the number of recruits is fixed, the relationship will asymptote and display nonlinearity because of density-dependent effects on survival (broken line). High-quality habitat will generally have higher survival rates, resulting in a steeper abundance–area relationship. Note that the horizontal axis can be any measure of habitat quantity (area, volume, stream discharge, etc.).

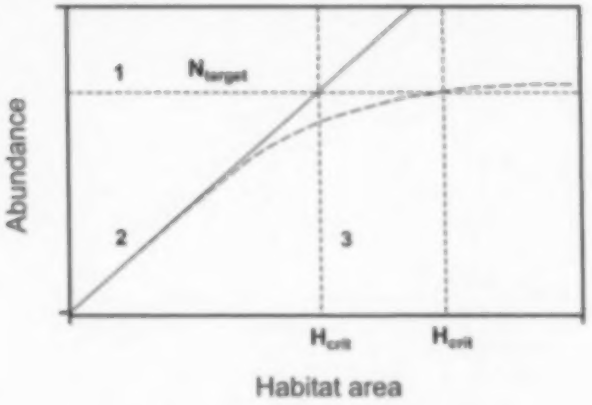
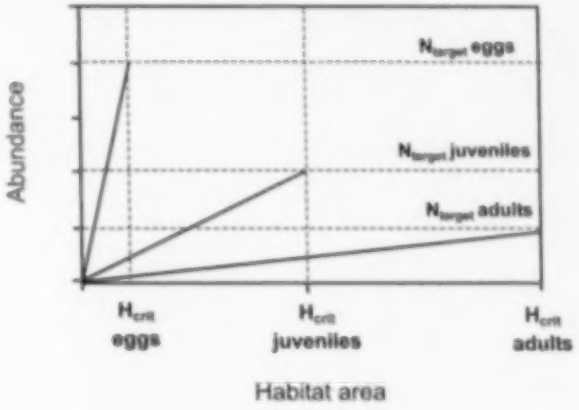


Fig. 2. For species with multiple life history stages, sufficient individuals need to recruit to each life history stage to meet the adult recovery target. When life history stages are dependent on different habitats, separate habitat–abundance relationships, stage-specific population targets, and critical habitat areas need to be defined to meet the adult population recovery target. Population targets for early life history stages will depend on stage-specific survival rates. Note that the habitat area required by different life stages will depend on species ecology, although this figure assumes that individual and cohort area requirements increase from eggs to juveniles to adults. Egg to juvenile and juvenile to adult survivals are set at 25% and 40%, respectively, for illustration purposes. N_{target}, a population recovery target; H_{crit}, the quantity of habitat required to meet the recovery target.



The third definition emphasizes that discrete habitat features will only persist if the processes that generate those features are maintained in a broader landscape context (e.g., river flooding, riparian inputs, etc.; Barinaga 1996; Imhof et al. 1996; Roni et al. 2002). This expands the suite of candidate habitats suitable for critical designation beyond those involved in population limitation to include habitats that are essential for maintaining critical habitat. For instance, removal of streamside forest may lead to excessive sedimentation and solar heating, degradation of water quality, and siltation of critical spawning habitat. We expand on the logic underlying these working definitions later in this review.

Finally, it is important to distinguish between general characteristics of critical habitat and the location of specific critical habitat areas (Canadian Wildlife Service 2005*a*). The definition of critical habitat under the Species at Risk Act, in contrast with US legislation, appears to permit the designation of both spatial areas with fixed coordinates as well as discrete habitat features that may shift through space or time. Identifying the general properties of critical habitat — for example, the characteristics of suitable spawning habitat (substrate size distribution, water temperature, etc.) — is also necessary to establish the range of conditions that need to be maintained within critical habitat for maintenance of function, and to provide benchmarks for restoration of degraded habitat (Lewis and Casselman 1996). The specific location of critical habitat (as opposed to its general characteristics) is also clearly essential from a management perspective (National Recovery Working Group 2004), as well as for modelling the effects of different habitat areas and configurations on population size and persistence.

The critical habitat concept

The core assumptions of critical habitat designation are a positive relationship between habitat and population size and that a minimum area is required to achieve a recovery target. For some species habitat may play a minor role in population limitation compared with other factors (e.g., predators, invasive species, disease). In this case, other limiting factors may modify the designation of critical habitat (e.g., refuges from predation may be limiting), or critical habitat identification may be irrelevant depending on the suite of threats facing a listed species, which must be thoroughly assessed in the early stages of recovery planning. For those species where habitat plays a key role in population limitation, the logical steps involved in identifying critical habitat are (1) identify a population recovery target; (2) define a quantitative relationship between habitat and population size; and (3) define sufficient habitat to meet the recovery target based on the habitat–population relationship (Fig. 1).

For species with multiple life history stages that use different habitats, this process will need to be repeated for each life stage (Fig. 2). This will require estimates of stage-specific survival (fraction of the population that successfully recruits to each life history stage) and separate relationships between habitat and abundance for each life stage (e.g., Minns et al.

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1996*a*; Nickelson and Lawson 1998). Although Fig. 2 is a simplistic representation of the complex habitat-explicit population models that may be required for some species, it provides a useful context for understanding the logic behind critical habitat designation, as well as a framework for identifying information gaps. Below we consider the information needs to achieve these steps in more detail.

Key information needs for identifying critical habitat

Basic organism life history

There are several core information requirements fundamental to any assessment of critical habitat. The first is a solid understanding of the life history and basic habitat associations of the species of interest (Regier 1976; Jamieson 2003; Rosenfeld 2003). Although preliminary assessment of critical habitat should proceed for those life stages where information is available, few credible inferences can be made concerning critical habitat when there are significant gaps in understanding of an organism's basic life history. If this information is lacking, research to establish basic habitat associations is the first priority (Randall et al. 2003), since habitat requirements of a poorly documented life history stage may be the primary factor limiting a population. This is of particular concern for species where different life stages use widely divergent (or spatially distinct) habitats, and is less relevant for species where all life stages share a common habitat.

Habitat availability

Inferences about habitat limitation require accurate information on the quantity and distribution of different habitats available to a species. Habitat information may range from basic distributional data (latitude, longitude, elevation) to detailed physical (temperature, rainfall) and biological characteristics (vegetation cover, soil types). Data sources may include remotely collected data (satellite imagery) or habitat features that must be identified in the field (e.g., spawning sites). The reliability of this information is fundamental to the credible assessment of critical habitat.

The appropriate metric of habitat availability is also a key consideration and may vary between species and ecosystems. Measuring habitat abundance is generally straightforward and any quantitative metric can be used (i.e., habitat area, volume, etc.). Lotic habitats, however, are somewhat unique in that the quantity of available habitat depends on the amount of water flowing in the stream channel. Since the quantity of different habitat types changes with discharge, defining the amount of limiting (critical) habitat required to meet the recovery target may require identification of specific instream flow needs (e.g., critical minimum flows), particularly in streams subject to regulation or water extraction.

Recovery targets

Clearly defined population recovery targets are integral to the identification of critical habitat (Canadian Wildlife Service 2005*b*). To make the case that a particular habitat is limiting a population and is therefore critical, the quantity of habitat designated needs to be related to a population benchmark, whether it be the current population size or a specific recovery target. This target may be either quantitative (e.g., 20 000 individuals) or qualitative relative to the present population (e.g., no decline). Quantitative targets can be either distributional (e.g., maintain the current or historic distribution of a species) and (or) population-based (e.g., a minimum adult population size of 8000 individuals).

While population recovery targets are required to determine the total amount of habitat needed for long-term persistence, they are not necessarily required for proactive designation of critical habitat for severely depleted populations. If a population is clearly below the minimum necessary for long-term survival (often a listing criteria), then all limiting habitat for that population can legitimately be designated as critical even in the absence of a recovery target. This habitat is the subset of critical habitat necessary to support the present population and is termed "survival" habitat (National Recovery Working Group 2004). Currently unoccupied habitat may have to be designated as critical to permit the population to increase to meet a recovery target; this additional habitat is designated "potential" habitat. Credible designation of full recovery habitat (survival and potential combined) requires both a population recovery target and sufficient understanding of habitat–abundance relationships to define the area of habitat necessary to meet the target.

Population recovery targets are usually set at a level that will ensure the long-term persistence of a species. This target may be arrived at in several ways. If sufficient data exist to parameterize a population model that incorporates temporal variability in demographic and environmental conditions, then a formal population viability analysis (PVA; Morris and Doak 2002) can be performed to establish a minimum recovery target. The validity of PVA has come under intense scrutiny as a method for assessing extinction risk (Coulson et al. 2001; Ellner et al. 2002; Reed et al. 2002), but it remains a useful quantitative tool for setting recovery targets and exploring how different management scenarios affect extinction risk (Brook et al. 2000; Haight et al. 2002), provided the results are interpreted with caution (Brook et al. 2002; Lindenmayer et al. 2003). However, sufficient information to perform a PVA is often lacking for listed species (Morris et al. 2002), usually because time and resources have not been available to obtain the necessary demographic parameters. In this case interim recovery targets need to be set based on available data until more accurate targets can be derived. One simple approach is to set recovery targets based on generic minimum viable population (MVP) sizes. Although early research in PVA suggested that MVPs should vary over a wide range depending on the biology of a species (Lande 1988; Simberloff 1988), recent evidence suggests that there is less variation in MVPs among different taxa than previously thought (e.g., Reed et al. 2003).

Thomas (1990) presents a general argument based on temporal population variability (probability of population decline below a threshold that could trigger extinction) that MVPs for species should be in the low to mid thousands, and suggested a mean recovery target of 5500 reproductively mature individuals. Reed et al. (2003) performed a more formal review of MVPs based on PVA of 102 vertebrate taxa (including one freshwater fish species) and observed a mean

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MVP of 7300 (± 560 standard error) adults and a median of 5800. Reed et al. (2003) concluded that MVPs on the order of 5000–7000 adults could be used as an interim recovery target for listed vertebrate species pending derivation of specific data to parameterize a more formal PVA.

The use of generic recovery targets needs to be tempered by several considerations. First, any interim recovery target based on a generic value should be adjusted up or down based on the known biology of a species and associated threats. Some species, such as the passenger pigeon (*Ectopistes migratorius*) or marine fishes (Hutchings 2001) may have much larger MVPs (hundreds of thousands) if, for example, large aggregations are required for successful reproduction or recruitment (Carlton et al. 1999). Conversely, for naturally rare endemics with a limited distribution, the intrinsic capacity of a habitat (as determined by pre-impact population size) may provide a natural limit to a recovery target that is well below a generic value. Second, the species used to calculate MVPs using PVA in Reed et al. (2003) were experiencing good habitat conditions; species that were in decline (i.e., experiencing negative population growth) were explicitly excluded from their analysis. Listed species are often in decline, indicating that the quality of habitat they are experiencing is below its historic mean. In this case, MVPs may be substantially larger than those recommended by Reed et al. (2003) because population growth rate (the ability of a species to recovery following a stochastic population decline) will be lower in poor-quality (e.g., degraded) habitat, increasing the probability of extinction and therefore the minimum population required for species persistence. Third, the relevance of the MVP as a recovery target will depend on the status of a species and its population trajectory. For species that are already below an MVP threshold, the MVP is a useful and compelling recovery target. For species that are in the early stages of decline and far above an MVP threshold, the broader goal of recovery planning is to first arrest the population decline and then take steps to move the population towards a recovery target, rather than to simply permit a population collapse towards a relict MVP (Olver et al. 1995). In this case, an appropriate recovery target could be well in excess of the MVP.

To some degree, recovery targets, as established by the recovery team, are and should be context dependent (Elphick et al. 2001). The MVP represents a minimum recovery target that cannot be compromised unless a species is deemed unrecoverable for biological, logistic, or economic reasons. However, recovery targets in excess of an MVP can be established if it is required to move a species to a lower risk category (as defined by quantitative listing criteria) or if the recovery team decides that, for instance, the reestablishment of a species throughout its former range is a legitimate long-term goal. In principle, recovery planning is intended to ensure emergency protection and management until species have recovered to a point where they can be delisted and routine management legislation and procedures can take over (e.g., Johnston et al. 2002). This may never occur for species that are endangered because of extreme natural endemism (Caughley 1994; Doremus and Pagel 2001), but is in principle possible for historically abundant taxa where the ultimate goal of recovery is to move a species to a lower level of endangerment (e.g., from endangered to threatened to special concern or not at risk).

Habitat–abundance relationships

Designation of critical habitat requires quantitative relationships between habitat and abundance, because these relationships are needed to establish the amount of habitat required to achieve a population recovery target. Biologists regularly develop relationships between habitat and organism abundance for management purposes or during basic ecological research. These are often fairly simple relationships between habitat area and population size (e.g., lake area vs. sockeye salmon (*Oncorhynchus nerka*) abundance (Burgner 1991) or total stream length vs. coho salmon (*Oncorhynchus kisutch*) smolt production (Bradford et al. 1997)). These examples represent very general relationships between population size and total habitat area that may be appropriate for identifying critical habitat in ecosystems with little spatial variation in habitat quality, or for endemics with very small ranges (see Appendix A).

When organisms are patchily distributed across a landscape, a finer resolution of habitat associations and critical habitat may be appropriate. Many studies have demonstrated that variance in abundance is related to variance in habitat type and quality (e.g., Pess et al. 2002), and critical habitat designations should occur at a scale that reflects this. The required resolution of habitat–abundance relationships and critical habitat designation will ultimately depend on the biology of the species being examined, and the spatial and temporal variation in its habitat. For example, designation of spawning habitat at the reach scale may be more appropriate than the channel unit scale if discrete riffle locations are periodically altered by floods.

The role of habitat in population limitation can best be understood by considering habitat effects at three spatial scales. At the smallest spatial scale, habitat type and quality affect the fitness (growth, survival, fecundity, reproductive success) of individuals. Understanding how habitat affects the performance of individuals is key for differentiating critical and noncritical habitat and for understanding the mechanisms whereby habitat change causes population-level effects (Hayes et al. 1996). At a larger spatial scale, the relative availability of habitat for different life history stages will determine the primary limiting habitat factor for a population, which life history stage it operates on, and the specific identity of critical habitat. For species with multiple populations, the size and spatial configuration of different habitats at a landscape scale and their status as sources or sinks will determine which habitats and subpopulations are critical for the persistence of the species as a metapopulation. The information required to define critical habitat and establish habitat–abundance relationships at any of these scales will depend on the biology and distribution of the species of interest, as described below.

Habitat effects on individual performance: assessing habitat quality

Habitat quality is a widely used but loosely defined concept in fish and wildlife management and is generally understood to represent the ability of a habitat to sustain

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individuals of a particular species and support population growth (Garshelis 2000). The biological response to habitat is then used to infer which features of habitat are important for organism growth and survival. Habitat quality is a function of the availability of prey, the abundance of competitors, predators, refuges, and a suite of other environmental attributes. Credible metrics of habitat quality (i.e., the density-independent biological response to habitat) are fundamental to the identification of critical habitat as well as most other stages of recovery planning. The best indices of habitat quality are direct measures of the fitness consequences to individuals (growth, survival, fecundity, reproductive success) of using different habitat types (Sogard 1994; Railsback et al. 2003) in the absence of competition (i.e., at low density). Production is the emergent population-level measure of habitat quality that integrates the effects of individual growth and survival (Randall and Minns 2000). Unfortunately, these metrics are often difficult to obtain, and biologists typically use more easily measured surrogates of habitat quality, such as presence or abundance.

The presence or absence of individuals in different habitat types is the simplest metric of habitat quality. However, it is potentially misleading (Garshelis 2000); for instance, Able (1999) found the presence of large numbers of subtropical juvenile fish in a New Jersey estuary to be a poor indicator of suitable rearing habitat, since most died at low fall and winter temperatures. Presence data may fail to distinguish between source and sink habitats (e.g., Able 1999), and provides no information on variation in quality of occupied habitats.

Measures of abundance (e.g., density, frequency of use, catch per unit effort) contain more information on habitat quality than presence or absence. Under the assumptions of Ideal Free Distribution theory (Fretwell and Lucas 1970), organisms should select habitats that maximize their fitness, resulting in the highest densities in high-quality habitat. However, density and habitat use can also be misleading indicators of habitat quality (Van Horne 1983; Hobbs and Hanley 1990; Garshelis 2000). Caution should be used when inferring habitat quality based on habitat use, particularly when mechanisms such as territorial behaviour can displace subordinates into poor-quality habitat at high densities (Van Horne 1983; Messier et al. 1990; Railsback et al. 2003). The long-standing discussion on the usefulness of habitat suitability curves (Bovee 1982; Rubec et al. 1999; Parasiewicz and Dunbar 2001) documents many of the problems inherent in the application of habitat use as an index of habitat quality (Mathur et al. 1985; Railsback et al. 2003). Density and measures of habitat selection may be of great utility in the designation of critical habitat, but their reliability may require validation if aspects of species biology (e.g., territoriality) warrant it. Arguably, when the consequences of being wrong may lead to extinction, a greater level of confidence in assessment of habitat needs is desirable.

Direct measurements of individual (or population) growth, survival, and fecundity in different habitats are the most reliable indices of habitat quality (Sogard 1994; Railsback et al. 2003; Rosenfeld 2003). However, vital rates associated with specific habitats are usually much more difficult to estimate than abundance and must either be measured in different habitat types in the wild (correlative approach) or by measuring performance of individuals experimentally confined to different habitats. Because growth rates in the wild are often density dependent, experimental manipulations may be necessary to reliably assess habitat quality. Measuring individual performance in different habitat types will be easier in some ecosystems than others. While it may be feasible to monitor growth and survival of individual fish confined to different habitats in streams (e.g., Lonzarich and Quinn 1995; Rosenfeld and Boss 2001), for example, it may be extremely difficult in other systems (e.g., marine pelagic), requiring that inferences about critical habitat be made with less data than might be acceptable elsewhere (e.g., Gregr and Trites 2001).

Limiting habitats for populations: habitat quantity

The relationship between population size and habitat illustrated in Fig. 1 is simplistic, but may adequately represent the dynamics of species where life stages share the same habitat. The ecology of most species is more complex, with different life stages often requiring different habitats (Fig. 2), which may or may not overlap in space (Schlosser 1991; Northcote 1997; Rieman and Dunham 2000). To meet a recovery target of adult animals, sufficient habitat must be available to support enough individuals to recruit to each sequential life stage. Critical habitat for each life stage can then be designated based on the quantity and quality of habitat necessary to achieve the recovery target. This is illustrated in Fig. 2, which shows population sizes and habitat–abundance relationships for three life history stages (eggs, juveniles, adults) of a hypothetical fish species. Understanding how habitat quality and quantity sequentially limit the abundance of different life stages is therefore fundamental to the identification of critical habitat (Imhof et al. 1996; Halpern et al. 2005). High-quality habitat will generally have higher survival rates, resulting in higher density and a steeper abundance–area relationship.

The probability that an individual will survive to reproduce will be the product of a series of stage-specific survivals that depend on habitat conditions (quality) experienced by different life stages (S_1-S_2-S_3,…S_n; Moussalli and Hilborn 1986). Survival at any life stage will also depend on density (i.e., density dependence will reduce survival at high densities so that the number of individuals recruiting to the next life history stage has a ceiling determined by the capacity of the habitat). Severe habitat limitation implies strong density dependence and therefore lower stage-specific survival. Increasing either density-independent survival (by increasing habitat quality) or the amount of available habitat will shift population limitation to a different life history stage (Bradbury et al. 2001; Halpern et al. 2005).

We illustrate a scenario (Fig. 3*a*) where there are sufficient adults to saturate spawning habitat, adequate egg survival to saturate juvenile-rearing habitat, and sufficient juveniles recruiting to the adult population to saturate adult habitat (with saturation meaning habitat that is at capacity, i.e., the point where density-dependent increases in mortality limit additional recruitment). Because adult habitat is at capacity in this scenario (i.e., adult habitat is limiting), the population will not respond to any increase in the availability of spawning or juvenile-rearing habitat. Increasing the availabilty of adult habitat will result in a compensatory population re-

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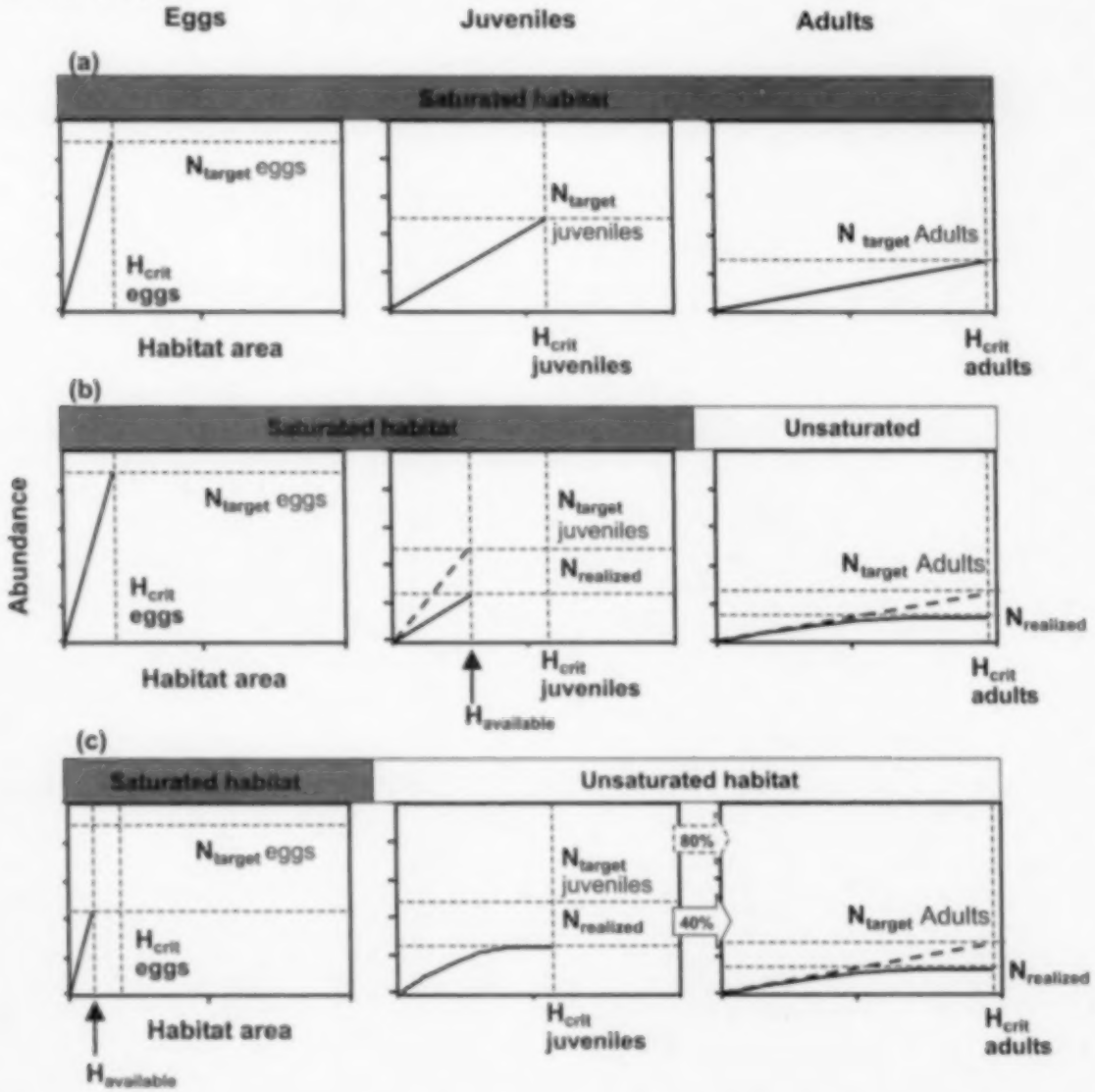
Fig. 3. Different scenarios of population limitation are illustrated for a hypothetical fish species with three distinct life history stages that use different habitats. The left panels illustrate the habitat–abundance relationship (solid line), stage-specific population target (horizontal broken line, N_{target}), and critical habitat area (vertical broken line, H_{crit}) for eggs; the middle panels illustrate this for juveniles and the right panels for adults. Figures represent abundance at a specific point in time, since densities of a cohort decrease over time. Egg to juvenile and juvenile to adult survivals are set at 25% and 40%, respectively, with an increase in stage-specific survival indicated by a broken arrow. (*a*) Habitats for all life history stages exist in an optimal ratio such that all habitats are at capacity (i.e., sufficient individuals recruit from each life history stage to saturate habitats for subsequent life stages to achieve the adult population recovery target). (*b*) Available juvenile rearing habitat ($H_{available}$, center panel) is insufficient to recruit enough juveniles ($N_{realized}$) to the adult life history stage to meet the adult recovery target (solid line). If it is impossible to increase the area of habitat available to juveniles, then increasing habitat quality (the slope of the habitat–abundance relationship; broken line) can increase juvenile recruitment to meet the recovery target. (*c*) In this scenario, the availability of spawning habitat is limiting the population below the recovery target. Increasing the area of habitat available to subsequent life history stages will have no effect because these habitats are unsaturated (under-recruited). However, increasing stage-specific survival (e.g., juvenile overwintering survival; broken arrow) will increase recruitment to the adult stage to meet the recovery target, despite habitat limitation at an earlier stage. This illustrates that populations can be limited by both habitat quantity and quality for different life history stages, providing an opportunity for multiple leverage points to achieve a recovery target.



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sponse (release from density dependence; Rose et al. 2001) that quickly attenuates because of insufficient recruitment to saturate adult habitat (e.g., curved line in Fig. 1). Depending on the strength of density-dependent processes, any significant increase in the adult population will require proportionally increasing habitat availability (recruitment) for earlier life stages as well. The ideal proportion of habitats for a particular species can therefore be thought of as existing in an optimal habitat ratio, which can be defined as the relative proportions of habitats for different life stages where all are at capacity. Optimal habitat ratios represent a potentially useful approach for conceptualizing the habitat requirements of species and for developing rules of thumb for habitat restoration (e.g., Reeves et al. 1989; Rosenfeld 2003).

When habitat for one life stage is in short supply, then that life stage and its associated habitat represent a limiting bottleneck for the adult population (Minns et al. 1996*a*). This will occur, for example, when available juvenile habitat is inadequate to produce sufficient recruits to saturate adult habitat (Fig. 3*b*, solid lines). Increasing the size of the limiting juvenile cohort can be achieved through either increasing the area of juvenile habitat or by increasing the quality of existing habitat so that the original number of juveniles can be supported in a much smaller area (Fig. 3*b*, broken lines). This example illustrates three points that are relevant to both designation of critical habitat and recovery of degraded habitats. First, increasing the area of habitat available to a life stage before or after a limiting stage will have no effect on the adult population; correct identification of the limiting stage is therefore essential to effective population recovery. Second, habitats other than the limiting one may also qualify as critical because they will become limiting once the bottleneck is removed (therefore classified as potential habitat; National Recovery Working Group 2004). Third, increased numbers of a limiting life stage can be achieved either through increasing the quantity or quality of available habitat or through a combination of both. This latter point is extremely important because it introduces flexibility in approaches for both designating and restoring critical habitat.

The idea that a single habitat or life stage can be a bottleneck for a population is misleading; it implies that habitat conditions for life stages subsequent to the bottleneck will not influence adult population size. However, increasing habitat quality for life stages subsequent to a bottleneck may have a positive and potentially profound effect on the ultimate population size. A population may therefore be limited by habitat quality at multiple life stages even though limited by habitat quantity at a single life stage. For instance, consider a scenario where a population bottleneck is created by inadequate recruitment from limited spawning habitat (Fig. 3*c*, solid lines). Even though spawning habitat is limiting, an improvement in juvenile overwintering habitat quality (arrows, Fig. 3*c*) may increase juvenile survival enough to achieve the adult recovery target (broken line, Fig. 3*c*). It is important to understand that populations may be limited by habitat quality at more than one life stage and that this creates multiple leverage points to increase population size within a life history. Which habitats are the most practical and efficient to manipulate will depend on the specific circumstances of each species at risk. For instance, when increasing the quality or quantity of limiting habitat is not possible, increasing quality (survival) for a later life history stage may be a practical management option. Key information needs for species at risk therefore include the determinants of habitat quality, how to improve them, and understanding quantitative effects of habitat quality on growth, abundance, and survival.

In practice, it is very difficult to identify which habitats and life stages are limiting a population. For example, Nickelson et al. (1992) used density of juvenile coho salmon in different habitat types during winter high flows to infer that highly selected backwater refuges were limiting smolt production in coastal streams. This was confirmed by demonstrating increased smolt abundance in watersheds subject to restoration of high-quality overwintering habitat (Solazzi et al. 2000). This example illustrates several points: first, the careful use of habitat selection (density) data, in conjunction with a good knowledge of life history, can provide useful insight into limiting habitat factors. Second, the only way to unequivocally demonstrate that a habitat is limiting is to show population-level effects of habitat change, often an expensive, time-consuming, and difficult proposition.

Habitat-explicit population models may be a more practical alternative for identifying limiting habitat, potential impacts of habitat change, and leverage points for recovery actions (Akcakaya 2000; Bradbury et al. 2001; Haight et al. 2002). Models can then be used to guide habitat management, and management activities can be treated as adaptive experiments to test hypotheses about population limitation (Walters and Holling 1990; Jones et al. 1996; Minns et al. 1996*b*) and to generate more realistic model parameters for management. This approach may be particularly appropriate for species at risk, where there is more impetus for careful management because the consequences of incorrect management are more serious than for unlisted species. The sophistication of models and the information required to parameterize them (and even their need in the first place) will ultimately be driven by the specific context of endangerment (see Appendix A), as well as the quantity of data available.

Habitat models range from simple models that generate population estimates by extrapolating densities of animals in different habitat types to larger areas (Hankin 1984; Hankin and Reeves 1988) to habitat-explicit, size-structured population models (e.g., Nickelson and Lawson 1998; Akcakaya and Atwood 1997; Railsback et al. 2003). Habitat-explicit population models are the most realistic for exploring the potential of different habitat configurations to meet population recovery targets. These models have the additional advantage that they can be used to generate PVA by including stochastic effects on demographic rates to assess time to extinction.

Metapopulation considerations: assessing which populations are critical

For species that exist as a metapopulation (a group of spatially disjunct populations linked by migration), some populations may be disproportionately important for the survival of the species. If all populations are required to meet a recovery target (or when an explicit recovery goal is to maintain the original distribution of a species), then critical habitat should be designated for each population. If only a subset of populations are required to meet a recovery tar-

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get, then it will be necessary to designate critical habitat only within this subset. One of the recovery tasks will therefore be to identify which populations are required along with their spatial configuration.

Distinguishing between source and sink populations is fundamental to identifying populations essential for species persistence. Failure to distinguish these may result in protection of sinks instead of sources, inappropriate identification of critical habitat, and underestimation of the probability of extinction. The subset of populations necessary for species persistence may include a combination of sources and sinks (Pulliam 1988; Pulliam and Danielson 1991) if sink habitats are corridors for dispersal or refuges for recolonizing source populations vulnerable to stochastic extinction. This is particularly relevant to species in streams and rivers (Schlosser 1995; Rieman and Dunham 2000; Labbe and Fausch 2000), which are likely to exhibit a metapopulation structure (i.e., subpopulations experiencing periodic extinction and recolonization). Sinks habitats may also qualify as critical if they can be transformed to source habitat through restoration or natural regeneration (Sinclair et al. 1995).

The importance of each population to species persistence will also depend on its size and associated threats. Extinction risk may arise from a suite of natural stochastic (e.g., climate extremes, floods) and anthropogenic events (e.g., pollution, urbanization, exotic species, etc.). On average, larger populations in high-quality habitat are less likely to go extinct from natural events than small populations in poor-quality habitat (Caughley 1994; Rieman and Dunham 2000). Unfortunately, human impacts are often concentrated in high-productivity habitats where populations would otherwise be most likely to persist (Kerr and Cihlar 2004; Harig et al. 2000; Allan 2004). In some cases (e.g., developed landscapes), the populations most likely to persist may very well be smaller low-productivity populations isolated from human impacts. Properly identifying threats for different populations is essential for determining which populations are critical for species persistence, and whether recovery actions need to focus on increasing population size and habitat quality or on reducing risk from human impacts.

Identifying critical habitat at the level of multiple populations may be most challenging when habitat loss is a minor factor in species endangerment, and when populations are limited by non-habitat factors such as overfishing or low ocean survival. Atlantic salmon (*Salmo salar*) on the east coast of Canada are a good example; there is abundant, unoccupied, freshwater rearing habitat for many (>30) discrete populations (Irvine et al. 2005), but it is unclear where to designate critical habitat in freshwater because of uncertainty in the spatial distribution of population recovery (should there be any). In the face of uncertainty, it may be appropriate to designate larger areas as critical than would be necessary if, for instance, freshwater rearing habitat was clearly limiting and there was reliable information on how different populations would contribute to meeting a recovery target. It should be noted that regulating fishing or otherwise increasing ocean survival is the conservation priority in this example, and critical habitat is largely irrelevant, especially if there are minimal threats to habitat. Critical habitat should eventually be defined so that if ocean survival increases, limiting habitat essential for population recovery is protected, but identifying critical habitat remains a secondary conservation priority in this scenario. Legal requirements aside, the effort that goes into defining critical habitat should be proportional to the benefit to the species.

Key information needs at the metapopulation scale therefore include (*i*) determining the status of discrete populations as sources or sinks, (*ii*) identifying corridors for dispersal and evaluating the probability of exchange between populations, and (*iii*) assessing the probability of subpopulation persistence based on risk of extinction from combined natural and anthropogenic impacts.

Habitat required to achieve the recovery target

When relationships between limiting habitat and organism abundance have been developed, the quantity and location of habitat required to meet the recovery target can be determined. The population size that can be supported by any given habitat will be the product of habitat area (quantity) and animal density (quality, assuming habitat is saturated). For endemic species limited by scarce habitat, all available habitat may be required to meet the recovery target (see examples in Appendix A). For more abundant listed species with wider distributions, various combinations of habitat areas of differing quality may support the target population. In effect, different areas may be substitutable in terms of their contribution to a recovery target. This will be a key issue for both critical habitat identification and recovery planning, since it allows flexibility in designation of critical habitat, which will be particularly important for species in developed landscapes where there are significant social and economic costs to designating critical habitat.

Evaluating the substitutability of candidate habitat patches requires careful consideration of the roles that habitat quantity and quality play in population persistence. Changes in habitat quantity influence carrying capacity (target population size), whereas habitat quality affects population and individual vital rates (i.e., growth, survival, and fecundity) as well as capacity (Hayes et al. 1996). Population viability is influenced by both habitat capacity and productivity; larger populations are more resistant to extinction from demographic and genetic stochasticity, while populations in high productivity habitats are more resilient because growth rates are higher following population declines. Ludwig (1999) noted that catastrophic population declines are natural phenomena in real populations, that this issue is usually ignored in PVA, and that this can lead to the probability of extinction being underestimated. Protecting high-quality (productive) habitat may therefore be an important factor for maximizing long-term population persistence (Nickelson and Lawson 1998). Substituting different high-productivity habitats may not affect long-term persistence, but substituting a large area of low-quality habitat for a small area of high-quality habitat with equivalent capacity may significantly increase risk of extinction (Fig. 4). While socio-economic issues will influence which habitat configurations are feasible, and it may not always be possible or necessary to protect the highest quality habitat, the consequences of substituting lower quality habitat need to be carefully considered.

It is worth noting that the quantity of habitat available will also affect recovery rate following a perturbation. Density-dependent processes will slow population growth as it ap-

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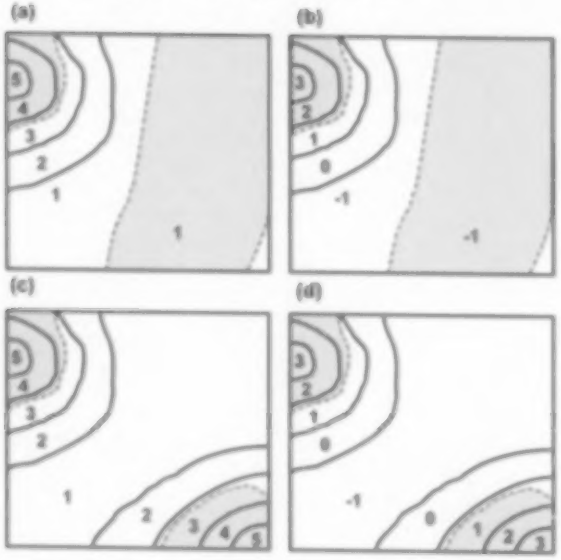
Fig. 4. Hypothetical landscapes where contours represent growth rate potential (habitat quality) for individuals or populations. Filled areas bounded by a dashed line represent candidate critical habitat areas. Right hand panels represent a shift in habitat quality associated with a stochastic climatic event or regime shift. In panel (*a*), a small area of high-quality habitat supports the same population as a large area of low-quality habitat, so that the patches appear to be superficially substitutable. However, when a large-scale climatic event reduces habitat quality equally across the landscape (panel *b*), the low-quality habitat becomes a sink with negative growth, while the high-quality habitat remains a source habitat, indicating poor substitutability. Panel (*c*) illustrates two high-quality patches that are truly substitutable, since habitat capacity is equivalent and both are equally resilient to stochastic changes in habitat quality (panel *d*).



proaches the recovery target and the carrying capacity of the habitat. Designating a larger area than necessary to achieve a recovery target will reduce density-dependent effects on growth and survival and ensure that the population reaches the target sooner, even though the final capacity of the habitat will exceed the recovery target. If minimizing recovery time following perturbation is critical for population persistence, then designating a larger area than required to meet the population recovery target may be justified.

The spatial configuration or proximity of alternative habitat patches (habitat complementarity; Dunning et al. 1992; Kocik and Ferreri 1998) will also be an important consideration for critical habitat selection. This applies to candidate habitats used by a single life stage, as well as habitats used by different life stages (*e.g.*, spawning vs. rearing habitat (Schlosser 1995; Kocik and Ferreri 1998)). For instance, juvenile-rearing habitat in close proximity to spawning habitat may function better than rearing habitat that is distant from spawning sites. Future threats from natural and anthropogenic factors should also be an important consideration when choosing among candidate critical habitats, since future threats will affect long-term average habitat value. For example, proximity to urban sprawl may compromise the future value of some candidate habitats, despite high quality in the present.

The appropriate scale of critical habitat designation will also depend on sensitivity of habitat quality to activities outside critical habitat boundaries. Species persistence may be compromised if habitat quality degrades from activities in the surrounding landscape (e.g., Sinclair et al. 1995; Fahrig 2001); this is a major concern for aquatic habitats that integrate impacts from the surrounding watershed. Regulation of activities outside of critical habitat must be sufficient to maintain quality inside critical habitat; when this is not possible, consideration should be given to expanding critical habitat boundaries to include the larger area. This is consistent with the Species at Risk Act, which permits critical designation for habitats that indirectly affect areas used by a listed species (Species at Risk Act 2002).

This highlights two opposite but complementary approaches to designating and managing habitat for species at risk: preservation vs. regulation. Preservation usually involves creating some form of protected area (with varying levels of effective protection; see Jamieson and Levings 2001; Bruner et al. 2001), while regulation is used for routine management of activities outside of protected areas. In most cases, the establishment of critical habitat over limited areas (preservation approach) will not ensure the persistence of a species, and regulation of activities in the broader habitat matrix surrounding critical habitat will be necessary (regulation approach). The issue becomes whether to designate as critical only those smaller habitats that will be preserved or to also include as critical habitat much larger areas in the surrounding matrix where activities will be permitted.

Key information needs for selection of specific critical habitat areas therefore include (*i*) sufficient information on habitat quality and complementarity to evaluate the substitutability of candidate habitat patches and (*ii*) the sensitivity of habitat quality to activities at different spatial scales (local vs. landscape), which will influence appropriate critical habitat patch size and acceptable activities inside and outside of critical habitat.

Summary

We have focused on the role of habitat limitation as the primary criteria for identifying critical habitat and advocated using some form of habitat–abundance relationship in conjunction with a population recovery target to define an appropriate area of critical habitat to support the target. We believe that this general framework will make critical habitat designations defensible, consistent, and transparent, all of which are essential elements for the management of species at risk.

Information requirements in this process framework can be summarized as follows:

(*i*) Fundamental information needs
- (1) Basic life history information, including identification of different life stages and their habitat associations
- (2) Availability of suitable habitat (present and potential)
- (3) Population recovery target

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(*ii*) Habitat–abundance relationships
- (4) Reliable metrics of habitat quality for different life stages
- (5) Relationships between habitat quality and quantity and abundance for each life stage

(*iii*) Habitat required to achieve the recovery target
- (6) Estimates of survival for different life history stages or sufficient demographic and spatial data to parameterize a PVA
- (7) Sufficient information on habitat quality and quantity to evaluate the substitutability and complementarity of candidate habitats
- (8) Severity of present and future threats to different habitats and subpopulations
- (9) Contribution of different subpopulations to species persistence

Informed management of fish and wildlife habitat must be based on an accurate understanding of habitat requirements, particularly for species at risk. Conservation efforts to protect critical habitat should be initiated with existing information to whatever extent possible; absence of information should not be an excuse for inaction (Ludwig et al. 1993; Pister 1999). Data acquisition to fill information gaps should clearly identify both short-term priorities (e.g., interim critical habitat designation) and long-term goals and applications (e.g., parameterizing a PVA). When it is necessary to make management decisions prior to filling key information gaps, established rules from the literature, information from similar species, or expert opinion may provide useful guidance (Randall et al. 2003; Martin et al. 2005). A precautionary approach will be appropriate when both uncertainty and the negative consequences of errors remain large. Even in relatively data-rich situations there may be considerable uncertainty, and it may be best to treat the relations used in various components of this process as hypotheses that should be tested and refined within an adaptive management framework.

Despite our emphasis on the role of habitat in population limitation, habitat may play a pivotal role in species persistence for reasons other than habitat limitation (e.g., maintenance of reproductive isolation between species). Critical habitat designation may be justified for a suite of reasons related to the biology and endangerment of particular species (see Appendix A, case 5).

Identifying critical habitat remains only one component in the broader process of managing endangered species. The other key component is the management of habitat and human activities outside of critical habitat. Activities beyond critical habitat boundaries will have a pervasive influence on species persistence for several reasons. First, habitat patches are intimately linked to their surrounding landscapes; activities in the broader habitat matrix often profoundly influence the quality of habitat in adjacent areas, particularly in aquatic systems. Second, protecting discrete habitats will fail to ensure their persistence if the landscape-level processes that create and maintain them (e.g., peak flows in streams) are not protected (Barinaga 1996; Fausch et al. 2002). If critical habitat areas are to be effective tools for species persistence, they must be complemented by careful management of land use in the broader landscape they are part of.

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Appendix A. Example taxa with contrasting informational requirements for identifying critical habitat.

A key issue with respect to identifying critical habitat is deciding on the necessary level of information to make a credible designation. Below we illustrate application of appropriate levels of rigour by considering scenarios for species along a gradient of increasing information need.

(1) Endemic species with highly restricted distributions

Many endangered species are listed because of highly restricted geographic distributions, which make them extremely vulnerable to extinction from stochastic events. The hotwater physa (*Physella wrighti*), a freshwater snail endemic to the Liard Hot Springs in British Columbia (Remigio et al.

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2001), is a good example. It is restricted to several hundred metres of stream and pool habitat (Te and Clarke 1985) and is thus highly vulnerable to habitat destruction or toxic contamination. In this example, simple distributional information is sufficient to infer the extent and location of critical habitat (i.e., presence or absence gives adequate information about habitat quality). Additional information in terms of density and vital rates within the occupied habitat is largely irrelevant for the identification of critical habitat, and the entire area warrants designation as critical for several well-defined reasons: (*i*) excluding occupied habitat from protection significantly increases extinction risk for extreme endemics; (*ii*) when a critical habitat area is small, the economic consequences (in terms of lost opportunity costs) of protecting the whole area vs. a subset are trivial; (*iii*) edge effects may render very small critical habitats ineffectual; and (*iv*) protecting areas at extremely small spatial scales (e.g., less than 30 m resolution) becomes problematic for management purposes.

Additional reasons to define habitat requirements beyond identifying the current distribution for an extreme endemic might include situations where (*i*) monitoring indicates the population is in decline, and the underlying mechanism is unknown; (*ii*) trends in climate are anticipated that might alter habitat quality and therefore population viability; (*iii*) there are plans to establish a population elsewhere, and information on habitat needs is essential for proper site selection and successful introduction (Harig and Fausch 2002). However, for the purposes of defining critical habitat, the known distribution of an extreme endemic should be sufficient.

(2) Broader endemic species where presence or absence gives inadequate information on habitat quality

For species that are not globally restricted to an extremely small area and are more widespread within one or several watersheds, it may not be desirable or necessary to designate as critical all habitats where the species is known to occur. Salish sucker (*Catostomus* sp.), which are endemic to 10 small watersheds in the lower Fraser Valley of British Columbia, are a good example; although widely distributed, they are only abundant in a subset of habitats (Pearson and Healey 2003). Because aquatic organisms often occur in sink or low-productivity habitats as a consequence of dispersal or displacement (e.g., Able 1999), presence alone may be an insufficient criteria for critical habitat identification and may potentially lead to the inadvertent inclusion of habitats that contribute little to species recovery. Worse still, it may lead to the inadvertent designation of sink habitats as critical. It may be appropriate to knowingly designate sink habitat as critical when there is an intention to restore sinks to sources as part of recovery planning (Sinclair et al. 1995), but this still requires the ability to differentiate between source and sink habitats. In this case, density or another abundance-based index of habitat quality is necessary to differentiate low- and high-capacity habitats and permit candidate critical habitats to be ranked in terms of their potential contribution to population recovery targets. For example, the density of Salish sucker was found to be consistently higher in deeper pool habitat, particularly marshes (Pearson 2004). In this case quantitative relationships between abundance and habitat features contribute essential information for identifying critical habitat and for informing appropriate design features for habitat restoration.

(3) Species where both presence or density are unreliable indicators of critical habitat

Under certain circumstances, both presence and abundance may be poor indicators of habitat quality. This will be the case when densities in the wild are too low for abundance to be a meaningful assay of habitat quality. This typically occurs when species are at risk because of recruitment failure, and an absence of larval and juvenile fish prevents reliable observations on early life history habitat associations.

Examples where low densities associated with recruitment failure complicate assessment of habitat needs include the razorback sucker (*Xyrauchen texanus*) and other endangered fishes endemic to the Colorado River (Minckley et al. 2003) and white sturgeon (*Acipenser transmontanus*) populations in the Kootenai River (Paragamian et al. 2001; Ireland et al. 2002). In both rivers, recruitment failure has been attributed to poor spawning success because of altered water quality, substrate, and flow regimes; predation on juveniles (particularly by alien species in the Colorado; Minckley et al. 1991); and habitat change. Evidence also implicates the importance of off-channel habitat for juvenile rearing, habitat that is now largely absent or unconnected with the river channel because of dikes and flood control downstream of dams.

When there are insufficient fish in the wild to infer habitat needs based on observed habitat use or when abundance is simply difficult to measure because of logistic constraints (e.g., challenges of sampling fish at low densities in very large rivers), some form of experimental manipulation may be required to assess habitat quality. These typically include observations of habitat selection by individuals released in the wild (e.g., using radiotelemetry) or individuals given the choice of alternate habitats in controlled experiments (Rosenfeld and Boss 2001), or by measuring growth or survival of fish experimentally confined to different habitat types (Rozas and Odum 1988; Lonzarich and Quinn 1995; White and Harvey 2001). Although radiotelemetry is an outstanding technique for identifying unique habitat such as spawning and overwintering sites, assessing frequency of habitat use through radiotracking is equivalent to using density (number of individuals found in a habitat type) as an index of habitat quality. Experimental releases of radio-tagged fish have been used on several occasions to assess habitat use by razorback sucker in the Colorado River (Gurtin et al. 2003; Mueller et al. 2003) and other endangered species (e.g., paddlefish, *Polyodon spathula*; Zigler et al. 2003). Experiments that measure actual growth and survival in different habitats tend to be more definitive in terms of understanding habitat quality because they directly quantify the fitness consequences of habitat use, but are more difficult to design and implement. Examples would include measuring growth and survival of fish experimentally confined to different habitat types in the wild (e.g., using enclosures or isolating fish in individual backwater habitats). Legal restrictions may preclude experiments that lead to mortality of endangered species, but the use of hatchery progeny (e.g., Ireland et al. 2002) or closely related species or populations not at risk may offer a partial solution to this problem. While the fitness consequences of habitat use to individuals provides

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strong insight into the role of different habitats for endangered species, the most definitive understanding of which habitats are critical will come from adaptive management experiments that measure the population-level consequences of habitat manipulations (e.g., Solazzi et al. 2000; Minckley et al. 2003).

(4) Species where sufficient data exists to parameterize habitat-explicit, stage-structured population viability analysis (PVA)

For some species, sufficient information may exist on habitat-abundance, growth, mortality, and production relationships to parameterize models that can explore both the population size and viability consequences of habitat change. While habitat-explicit PVA models are the ideal tools for modeling alternative scenarios for identifying critical habitat, the level of information required will probably only be available for species with extensive research histories. This usually includes species with significant historical or current commercial value. Salmonid species are a good example, and the wealth of information and the potential to transfer parameters among species facilitates model construction. Nickelson and Lawson (1998) provide a good example of a full life cycle, habitat-explicit PVA for coho salmon (*Onchorhynchus kisutch*) that explores the consequences of habitat degradation for stock viability. Other examples include several for birds (e.g., Akcakaya and Atwood 1997), fish populations in the Great Lakes (e.g., Minns et al. 1996*a*), and Atlantic salmon (*Salmo salar*; Legault 2004), although very few account for spatial variation in habitat quality. While PVA may be the most sophisticated planning tool for identifying critical habitat that scientists and managers can work towards, most endangered species will initially have insufficient data to parameterize complex models, and interim critical habitat designation may be necessary based on available data.

(5) Species where critical habitat is unrelated to population limitation

In some instances, critical habitat will be unrelated to population limitation, and measures of fish abundance or performance in different habitat types may be of secondary importance to critical habitat identification. This will be the case when habitat plays a role in species persistence other than simply limiting population size. Endangered stickleback species pairs (*Gasterosteus* spp.) in British Columbia (Schluter and McPhail 1992; McPhail 1993) are a good example. Sympatric species of benthic and limnetic stickleback have co-evolved in a handful of lakes, where the benthic species has morphological and ecological adaptations for feeding on benthic invertebrates in the littoral zone, and the limnetic species has adapted to feeding on zooplankton in the pelagic zone. Benthic and limnetic species coexist with limited gene flow because of strong reproductive isolation associated with accurate mate recognition and reduced hybrid fitness. Benthic and limnetic breeding males have different breeding colours, in addition to differences in size (benthics are much larger) and morphology that females use to identify conspecifics. Hybrids are fertile but selected against because they are less fit than either parental type, owing to intermediate morphology and lower reproductive success (Hatfield and Schluter 1999). Habitat is thought to play a key role in maintaining reproductive isolation because benthic and limnetic species nest in different habitats, water clarity influences light transmission and perception of nuptial colours (Boughman 2001), and larger prey items in the littoral zone may contribute to the greater body size of benthic species (a key factor in mate recognition).

Recently, hybridization rates have increased to the extent that the species pair in one of the lakes appears to have collapsed into an undifferentiated hybrid swarm (Kraak et al. 2001). Although a definitive cause is still lacking, habitat change (loss of macrophyte beds, changes in water clarity) associated with introduced crayfish (*Pacifastacus leniusculus*) is suspected. Increases in turbidity, loss of differential productivity between benthic and limnetic habitats that maintains a size differential between reproductive individuals of different species, and loss of nest site segregation have all been implicated as potential factors contributing to breakdown of reproductive isolation (presently an area of active research). For instance, increased turbidity might impair detection of nuptial colours and cause increased hybridization independent of effects on population limitation (Seehausen et al. 1997; Boughman 2001; Wood 2003). In this scenario, introduction of an alien species is the ultimate driver of hybridization, but impacts are largely mediated through habitat change. While management priorities should address control of the alien crayfish, and habitat likely plays some role in population limitation, critical habitat designation for stickleback species pairs needs to be primarily based on the role of habitat in maintaining reproductive isolation.

Although we have emphasized the role of habitat in population limitation as the primary criteria for identifying critical habitat throughout this paper, this example emphasizes the importance to critical habitat designation of clearly identifying the cause of species endangerment (e.g., population limitation vs. hybridization) and the role (if any) that habitat plays in it. While limiting habitat will be the primary reason for designating critical habitat for most species, designation will remain justified for a wide range of reasons unique to the endangerment of different taxa.

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PERSPECTIVE / PERSPECTIVE

Incentive-based approaches to sustainable fisheries

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Abstract: The failures of traditional target-species management have led many to propose an ecosystem approach to fisheries to promote sustainability. The ecosystem approach is necessary, especially to account for fishery–ecosystem interactions, but by itself is not sufficient to address two important factors contributing to unsustainable fisheries: inappropriate incentives bearing on fishers and the ineffective governance that frequently exists in commercial, developed fisheries managed primarily by total-harvest limits and input controls. We contend that much greater emphasis must be placed on fisher motivation when managing fisheries. Using evidence from more than a dozen natural experiments in commercial fisheries, we argue that incentive-based approaches that better specify community and individual harvest or territorial rights and price ecosystem services and that are coupled with public research, monitoring, and effective oversight promote sustainable fisheries.

Résumé : Les échecs des aménagements traditionnels centrés sur les espèces-cibles ont incité plusieurs chercheurs à proposer des approches halieutiques basées sur les écosystèmes pour favoriser les pêches durables. L'approche écosystémique est nécessaire, en particulier, pour tenir compte des interactions pêche–écosystème; elle ne suffit pas,

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cependant, par elle-même pour régler deux facteurs importants qui contribuent à rendre les pêches non durables : les incitations insuffisantes pour les pêcheurs et la gestion inefficace souvent présente dans les pêches commerciales développées qui sont régies principalement par des limites à la récolte totale et par des contrôles d'entrée. Nous croyons qu'on doit mettre beaucoup plus l'accent sur la motivation des pêcheurs dans la gestion de la pêche. En utilisant des données provenant de plus d'une douzaine d'expériences naturelles de pêche commerciale, nous cherchons à démontrer que des approches fondées sur les incitations qui précisent mieux la communauté, les récoltes individuelles et les droits territoriaux et qui évaluent aussi financièrement les services de l'écosystème, couplées avec de la recherche gouvernementale, de la surveillance et de la gestion efficace, promeuvent les pêches commerciales durables.

[Traduit par la Rédaction]

Introduction

Marine ecosystems are in global decline (Pauly et al. 1998; Buckworth 2001; Schiermeier 2002). The main cause is unsustainable fishing practices (Hannesson 2002) that arise from the following six principal factors: (*i*) inappropriate incentives; (*ii*) high demand for limited resources; (*iii*) poverty; (*iv*) inadequate knowledge; (*v*) ineffective governance; and (*vi*) interactions among fishery sectors and other aspects of the environment (Food and Agriculture Organization of the United Nations (FAO) 2002*a*).

In response to fisheries failures and a fall in the total catch in marine capture fisheries (Hilborn et al. 2003), many have proposed an ecosystem approach to fisheries (EAF) that gives greater weight to integrated management and emphasizes the importance of maintaining ecosystem health for future generations (Ecosystem Principles Advisory Panel 1999; Busch et al. 2003; Browman et al. 2004). While EAF highlights the importance of fishery–ecosystem interactions and knowledge gaps, with a few exceptions (ICES 2005*a*), it overlooks the importance of fisher behavior and incentives for fisheries management.

In this paper, we examine what can be done to mitigate the factors that contribute to unsustainability in commercial and industrial fisheries. Our focus is on inappropriate fisher incentives and ineffective governance, and we argue that a much greater emphasis should be placed on fisher motivation when managing marine resources (Larkin 1978). We propose incentive-based approaches to sustainable fisheries (IAFs) to complement EAF and existing management approaches that promote sustainability. We contend that fishers need economic rights and accompanying responsibilities, as well as price signals, to provide incentives for individual and collective action that promote more sustainable fishing practices.

The ecosystem approach: necessary, but not sufficient

The goals of ecosystem-based management are to promote healthy and resilient marine ecosystems and sustainable fisheries (FAO 2002*b*; Garcia et al. 2003). A key component of this approach is the conservation and protection of key habitats that are critical for ecosystem and population processes (Pikitch et al. 2004), primarily through the enforcement of marine reserves and no-take areas (Garcia et al. 2003). Reserves can lead to increased abundance, size, and biodiversity (Halpern 2003), as well as a more fecund population (Palumbi 2004) within no-take areas, and can potentially increase harvests in exploited areas via fish migration (Roberts et al. 2001; Gell and Roberts 2003). No-take areas are particularly helpful in the face of uncertainties (Lauck et al. 1998) and can also promote resilience to shocks and raise profitability, even when harvesting is optimal (Grafton et al. 2005). Despite these benefits, reserves only address some of the problems in fisheries (Allison et al. 1998; Leal et al. 2005) and do nothing to overcome key contributors to unsustainability, such as overcapacity. Reserves also do nothing to provide incentives for fishers to take into account the full impact of their harvesting practices on fisheries.

Other aspects of EAF include the use of the precautionary approach and the management of target and non-target species within the broader context of overall marine ecosystems, paying particular attention to bycatch, discarding, and habitat destruction (Pikitch et al. 2004). We endorse these approaches and the goals of ecosystem-based management but contend that a shift in priorities from target species to ecosystems (Pikitch et al. 2004) by itself does not recognize the importance of fisher behavior and their motivations (Hilborn 2004). Unless fisher incentives and associated governance arrangements are compatible with long-term goals of sustainability (Hilborn et al. 2005), EAF, or any other alternative to traditional, commercial fisheries management, will fail to prevent overharvesting of stocks or change fishing practices that damage habitat.

Failures of traditional, commercial fisheries management

The traditional approach to commercial fisheries management restricts fishing inputs and imposes total catch limits in an attempt to control fishing mortality. Input controls increase the costs of fishing and frequently fail in their objective to limit fishing effort because harvesters are often able to substitute unregulated inputs for controlled ones, causing a gradual expansion of effort, referred to as effort creep (Wilen 1979; Scott and Neher 1981). Competitive total allowable catches (TACs) in input-controlled fisheries also provide incentives for fishers to race against each other for a share of the catch before the total harvest limit is reached. Such racing behavior frequently results in fishers investing in unregulated inputs to increase their effective fishing capacity at the expense of others. In turn, these investments and the race to fish increase overall harvesting costs, lower the total net returns from fishing and jeopardize the sustainability of fisheries.

The traditional approach to commercial fisheries management fails to address the technical change that makes fishing more effective over time (Squires 1992) and does not instil a long-term perspective in fishers. For example, in the North Sea cod (*Gadus morhua*) fishery, some harvesters oppose reductions in the total allowable catch, despite the fact that the

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spawning stock is below a level that demands a harvesting moratorium (European Environment Agency 2004). In Canada's northern cod fishery, the regulator's concerns that reduced harvests would generate bankruptcies and unemployment, coupled with uncertainties over the status of stocks (Fisheries and Oceans Canada 2004*a*) and overestimation of stocks and recruitment (Walters and Maguire 1996), resulted in the TACs being set too high and was a major contributor to stock collapse in the 1990s (Hutchings and Myers 1994).

The negative consequences of input controls, whether they are applied to traditional target-species management or ecosystem approaches, are illustrated by the recent experience in Australia's federally managed fisheries. In the past 10 years, the Australian federal government has committed US$60 million per year to fisheries research and ecologically sustainable development, undertaken substantial buybacks of fishing effort, implemented detailed scientific fishery management plans that incorporate strong stakeholder involvement, and expanded its National Representative System of Marine Protected Areas (McLoughlin and Findlay 2005). Despite such strategies, fishers have successfully lobbied against recommended reductions in the TACs (McLoughlin and Findlay 2005). This lobbying, combined with effort creep in some input-controlled fisheries (Kompas et al. 2004), have contributed to a threefold increase in the number of Australian Federal fisheries classified as overfished in the past 10 years (Caton and McLoughlin 2005).

A similar story can be told in many other developed fisheries, even when the primary stated objective of management is to conserve fish stocks. Maguire (2003) observes that inappropriate incentives, inadequate and overly complex governance, and lack of knowledge are the main causes of the unsustainable harvesting of demersal fisheries in the North Atlantic. In these fisheries, despite the focus on the bioecological component of sustainability, management systems have frequently failed to achieve the desired outcomes. Ongoing effort creep has also led, in some jurisdictions, to an escalating complexity of rules as regulators try to close off the loopholes, leading to confusion and making enforcement difficult (Healey and Hennessey 1998). Resolving these challenges requires major changes that include a precautionary approach to management (FAO 1996), more transparent and participatory management, and a greater emphasis on incentives and rights for fishers (Maguire 2003).

Incentive-based approaches

The failures of traditional management suggest not only that total harvests must be set appropriately, but also that the greatest marine predator, fishers, be provided with the incentives to fish sustainably. A key to creating incentives for more sustainable behavior is to provide fishers with more secure harvesting or territorial rights to fish. Such rights enable fishers to enjoy a sustainable flow of benefits from fishing with an enforceable right to exclude others from these benefits but generally do not give ownership over the resource stock. Fishing rights may take several different forms (The World Bank 2004) and include individual harvesting rights (Scott 1999*a*), community- or group-based rights (Baland and Platteau 1996), and territorial user rights (Christy 1999; Sharp 1998).

Economic fishing rights are commonly viewed as a recent innovation, at least in terms of individual harvesting rights, but they have existed for centuries. For example, in Oceania, no-take areas, territorial user rights, and cooperative management ensured sustainable fisheries for centuries by allowing clans or families to control, for their benefit, reef and lagoon areas (Johannes 1978). The success of traditional marine tenure suggests that a key to generating appropriate incentives is for fishers to have the ability to exclude others from fishing, thereby reaping both the pain of overexploitation and the gains from conservation. Exclusive property rights, however, do not guarantee sustainability. In extreme cases, it may be economically rational to mine a fishery (Clark 1973), and if the holders of rights are large in number and with diffuse interests, incentives may still remain to cheat and take advantage of the conservation efforts of others. All fisheries are also subject to irreducible uncertainties (Ludwig et al. 1993) that make it difficult to set sustainable harvests and to understand the long-term impacts of fishing practices.

Incentive-based approaches make management more robust by ensuring, in most cases, that those who have the greatest impact on fisheries have an increased interest in their long-run conservation and directly bear the cost of overexploitation. We review the contributions of incentive-based approaches to sustainable fisheries in the following subsections.

Rights and responsibilities

The key to IAFs is to provide harvesters with long-term and secure rights (Hannesson 2004) that are legally enforceable, along with corresponding duties by nonowners to not interfere with these rights (Cole and Grossman 2002). In practice, individual harvesting rights are often specified as a revokable privilege, although New Zealand is a notable exception (National Research Council 1999). However, these privileges are de facto economic property rights, provided that adequate monitoring and surveillance exists. Control and enforcement should also ensure that the holders of the harvesting rights meet their responsibilities under the FAO's Code of Conduct (FAO 1995; Symes 2000), while fishers without such rights, or other privileges, are excluded from harvesting.

Secure and durable harvesting or territorial rights, in most cases, provide fishers with two incentives: they protect the value of their assets and also encourage the greatest possible sustainable flow of benefits from fishing. These incentives are complementary and occur concurrently, but the former is likely to be manifested in forms of collective action, whereas the latter manifests itself in individual actions. Individual efforts by fishers to maximize their net returns indirectly contribute to sustainable fisheries by improving economic performance and reducing the problems of overcapacity, while collective actions involve direct attempts to ensure sustainability by improving management decision making, the quality of scientific advice, and the monitoring of fisher behavior.

At the individual level, quantified fishing rights encourage fishers to harvest their fixed catch at lowest cost, to increase the value of landings through better handling and care of fish (Campbell et al. 2000*b*; Rice 2003; Dupont et al. 2005),

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or to change product form (from frozen to fresh), as occurred in the British Columbia (BC) halibut (*Hippoglossus stenolepsis*) fishery (Casey et al. 1995; Herrmann 1996). Such efforts, and the transferability that allows more profitable fishers to harvest a larger share of the total catch, improve efficiency (Grafton et al. 2000) and increase productivity (Fox et al. 2003*a*). Transfers of individual harvesting rights, in many cases, also help reduce overcapacity (Dupont et al. 2005), which is a major contributor to overexploitation of fisheries and poor economic returns for fishers.

Individual rights and collective action

A long-term interest in the fishery in the form of harvesting rights can encourage collective action to ensure management practices are consistent with maintaining the long-term value of these rights. By itself, greater participation in management decision making by fishers is not sufficient to promote sustainable fisheries, but we argue that sustainability is promoted by fisher participation in combination with more secure harvesting rights. Individual harvesting rights also provide a way to allocate joint management costs and thus help overcome the underprovision of services that benefit all fishers (Scott 1993).

There is evidence that individual harvesting rights can promote collective action in shellfish, demersal, and pelagic fisheries (Shotton 2001). For example, in the New Zealand east coast rock lobster (*Jasus edwardsii*) fishery, the introduction of individual harvesting rights prompted commercial stakeholders to initiate a locally focused fishing strategy. The industry successfully requested the regulator to lower the commercial catch and to restrict harvesting to a shorter winter period to make widespread illegal fishing easier to detect (Breen and Kendrick 1997). These and other fisher-initiated management measures have resulted in a dramatic stock recovery and substantially higher quota values (Leal et al. 2005). Similarly, in 2001, the scientist contracted by the Canadian Sablefish Association (CSA), an organization of commercial fishers with individual harvesting rights, advised of rapid declines in sablefish abundance. Shortly thereafter the CSA recommended to the regulator that the total catch be immediately reduced as a precautionary measure. Subsequent stock recovery that followed a decline in the TAC by almost 50% has allowed CSA members to benefit from their conservation efforts. In the Tasmanian abalone fishery, individual quota holders with direct involvement in advising the regulator successfully lobbied for large reductions in the total catch in the late 1980s. This allowed the stock to rebuild, and the quota holders were the principal beneficiaries of subsequent increases in the total harvest (Tasmanian Abalone Council 2003). The successful rebuilding of the Icelandic herring (*Clupea harengus*) stocks, through cuts in the TAC, were also strongly supported by industry because fishers wanted to protect the asset value of their harvesting rights (Hannesson 1996).

Individual harvesting rights can provide greater incentives for more bottom-up decision-making processes and opportunities for increased participation (Lane and Stephenson 2000). Indeed, if the creation of rights promotes economic sustainability, for which there is abundant evidence in the form of case studies (Davidse et al. 1997; Kaufmann et al. 1999; Shotton 2001), it is not surprising that holders of such rights would be prepared to invest their time and effort to protect their flow of benefits from fishing. This may take the form of funding for more on-board and dockside surveillance, increased research to improve the quality of scientific advice, and greater participation in management decision making. For example, in the BC sablefish (*Anoplopoma fimbria*) fishery, managed by individual harvesting rights since 1990, fishers initiated and funded research on trap escape rings that dramatically reduced juvenile capture and mortality. After individual harvesting rights were introduced in BC's halibut fishery, harvesters (through their industry association) set up and paid for dockside monitoring that tags every fish (Grafton et al. 2000). Similarly, in the BC groundfish trawl fishery, also managed by individual harvesting rights, fishers are strong supporters of science and have contributed millions of dollars to research (Rice 2003). Elsewhere, such as in New Zealand's fisheries, which have been managed by individual harvesting rights since 1986, fishers make important financial contributions to management through their associations and are also active participants in some fisheries research (Lydon and Langley 2003).

Group rights and collective action

Collective action can be encouraged in a number of different ways such as allowing fishers to organize and express their concerns to managers (Pomeroy and Berkes 1997) and participate in fisheries research and management (Rice 2001). Collective action can also be promoted through the allocation and support of harvesting rights for groups and to communities (Baland and Platteau 1996; Willmann 1999). For example, the Canadian government has created seven geographically based community management boards for the fixed-gear groundfish fishery in Nova Scotia. Each of these boards is charged with developing community harvesting plans and controlling the fishing activities of members (Peacock and Hansen 1999). This enables local knowledge to inform allocation decisions and prevents a one-size-fits-all approach to fisheries management.

The potential benefits of collective action with group rights is shown by purse seine fishers who recently established a cooperative in Alaska's Chignik salmon (*Oncorhynchus nerka*) fishery following a change in regulations passed by the Alaska Board of Fisheries. In a 2002 survey of all cooperative members, 67% claim that it has made them financially better off, 100% state that it has improved fish quality, and 88% consider it to have been either a very positive or a somewhat positive change in the management of the fishery (Knapp et al. 2002).

Numerous examples show that both community and group rights can improve management outcomes with collective action (Ostrom et al. 1994; Baland and Platteau 1996; Dietz et al. 2003). These actions are facilitated by social capital within communities and by trust between management authorities and fishers (Pretty 2003; Grafton 2005), but social capital does not necessarily require the existence of individual or group harvesting rights (Dietz et al. 2003). For instance, trust between scientists and fishers in the BC rockfish (*Sebastes* spp.) fishery in the 1990s led to new hypotheses and novel ways for testing them (Stanley and Rice 2003). It also contributed to a constructive advisory process that included an official working group with members from

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the industry and the regulator (science and fisheries management) that was established before the introduction of individual harvesting rights in the fishery (Rice 2003).

Participatory management and the allocation problem

Examples of effective participatory management in fisheries in which fishers bear the consequences of failures, as well as successes, should not be taken as proof that greater participation by fishers in management always generates better fisheries outcomes. We contend that participatory management, coupled with a failure to resolve the allocation problem (i.e., who gets what), may actually generate poorer sustainability outcomes and allow special interest groups to negatively influence management authorities as fishers compete for control of allocation mechanisms. For example, under the US 1977 Fishery Conservation and Management Act, power sharing among the federal government, fishers, and other stakeholders has occurred through Fishery Management Councils (FMCs). Turner and Weninger (2005) find that this particular system of voluntary participation in the regulatory process leads to over-representation by industry members with extreme preferences. Not surprisingly, this deconcentration of management authority has not been viewed as a success (Pomeroy and Berkes 1997). It has also been plagued by conflicts of interest (Allison 2002), and some FMCs appear to have sacrificed long-term conservation for short-run economic considerations (Parsons 1993).

At least in the case of the United States, a consultative system and delegation of management authority to fishers and other resource stakeholders, in the absence of appropriate fisher incentives and resolution of the harvest allocation problem, has contributed to rent-seeking behavior and conflicts among different interest groups. This has made decision making less, rather than more, effective (Mikalsen and Jentoft 2001).

Incomplete harvesting rights

An important issue when establishing harvesting rights is to ensure that they do not create perverse incentives that distort behavior and produce undesirable outcomes. This demands that rights for commercial fishers be as comprehensive as possible to avoid transfer of effort to non-quota species and that all commercial fishers are included. In Iceland, for example, exemptions from individual catch quotas for vessels under 10 gross registered tonnes, until they were abolished in 1990, distorted the composition of the fishing fleet and encouraged investment in smaller vessels (Arnason 1995). A similar increase in investment and catch has also occurred with the Icelandic longline fleet because half of the demersal catch has been exempt from quota restrictions during the months November to February.

Conflicts between commercial and recreational fishers can also be aggravated if the commercial fleet is subject to individual output controls but the recreational sector is not. For example, if individual rights only exist in the commercial fishery and if fish stocks are under pressure because of the expansion of the recreational catch, then the regulator may be tempted to reduce fishing pressure by simply reducing the commercial TAC. This undermines the commercial right, creates uncertainty for investment, and generates protest from the commercial sector. Such commercial–recreational conflicts, however, are not unique to fisheries using individual rights, nor do they necessarily imply that recreational fishers should be included within an individual quota management system in which the widely dispersed interests would generally make the transaction costs associated with trading and enforcing such rights prohibitive. Limits might be better specified for the recreational sector in other ways by, for example, imposing a mix of recreational fishing licences and individual daily bag limits. Such controls, however, may need to be supplemented with other methods such as spatial allocations that keep bulk fishing methods away from favored recreational sites.

Multiple target species

The incentive-based approach is applicable to fisheries in which there are few, or many, target species. A major concern, however, is that harvesters may have little ability to separately target each species. Consequently, the catch mix of fishers may not match individual quota allocations, which in turn may contribute to discarding and misreporting (Squires et al. 1998). A limited ability to target specific species may also result in undesirable individual quota underages and overages and also severely constrain fishers' profitability if total harvests of target species are restricted to prevent the overexploitation of vulnerable bycatch species (Squires and Kirkley 1996). Another issue with multiple target species is that if harvesting rights are only assigned to a subset of target species, then the transfer of fishing effort to target species without individual harvest controls may be encouraged (Dupont and Grafton 2001).

Although multiple target species make fisheries much more difficult to manage, especially with the setting of TACs, the ability of fishers to target individual species is not as constrained by technology as is commonly believed. Given appropriate incentives, fishers are able to adapt their fishing practices to reduce bycatch and adjust their species mix, even if the technology remains essentially unchanged. For example, purse seine vessels in the eastern Pacific were able to reduce dolphin (*Stenella* spp., and *Delphinus delphis*) mortality from over 130 000 in 1986 to less than 4000 in 1993 by changing fishing practices but using the same fundamental technology (Hedley 2001). In the BC groundfish trawl fishery, onboard observers record fishery mortality rates by species that count against quota owned or leased by fishers. This created an incentive for fishers to avoid catching less desirable species, and led to greater communication among skippers to avoid harvesting in areas where there was a high incidence of unwanted species. Fishers have also changed their behavior by using shorter tows, checking their nets more frequently, and employing test tows before fishing (Grafton et al. 2006).

Discards and bycatches

IAFs allow fisher incentives to be compatible with long-term conservation, but do not guarantee that all fishing practices promote sustainability. There have been cases in which fishers with individual harvesting rights have dumped lower valued fish to maximize the value of their trip landings (Parsons 1993; Arnason 1994; Squires et al. 1998), although such problems also exist in open-access and input-regulated fisheries (Leal et al. 2005), especially those regulated by trip

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and (or) vessel-size restrictions. However, discarding problems with individual harvesting rights can be mitigated and adaptively managed with appropriate incentives and instruments.

In the BC groundfish trawl fishery, which has been managed with individual harvesting rights since 1997, fish dumping is recorded by observers on all vessels and is counted against individual quotas. This quota reconciliation provides harvesters with the incentive to be much more selective in their fishing practices. As a result, the ratio of at-sea releases to the landed fish weight has greatly declined (Grafton et al. 2006). Recently, fishers have, on their own initiative, undertaken research that halved the fishing mortality of boccaccio rockfish (*Sebastes paucispinis*), a bycatch species that was designated as being at risk in 2002 by the Committee on the Status of Endangered Wildlife in Canada and for which harvesters do not have specific species quota (Fisheries and Oceans Canada 2004*b*; Fisheries and Oceans Canada 2005). This protects their livelihood because, should the boccacio be listed as requiring protection by the federal cabinet under Canada's 2003 Species at Risk Act (SARA), groundfish trawl fishing could be prohibited if current practices compromise the rapid recovery of the species and if Incidental Harm Permits were not issued to allow boccacio bycatch (Rice 2003).

Overcapacity and buybacks

The potential payoffs from IAFs include better protection of fish stocks and the environment, increased returns to harvesters (Dupont and Grafton 2001; Fox et al. 2003*a*; Dupont et al. 2005), and reduced fishing capacity (Grafton et al. 1996; Dupont et al. 2002). These benefits arise because secure and durable rights to fish, individually or communally, reduce racing behavior. In contrast, in input-controlled fisheries, the race to fish results in excess effort, substitution of unregulated inputs (Squires 1987), and lower overall net returns (Dupont 1990). For example, in the northern prawn (*Penaeus* spp.) fishery of Australia, the imposition of effort controls in the form of combined engine size and hull length restrictions encouraged fishers to increase the headrope length of their trawls to maintain their effective fishing capacity. Unfortunately, this substitution lowered technical efficiency and raised the cost of fishing while failing to prevent effort expansion (Kompas et al. 2004).

Top-down input controls also promote an us-versus-them attitude with managers (Charles 1995) and frequently fail to limit fishing effort (Townsend 1990) because the underlying incentives to race to fish are unchanged. As a result, over the period of 1970 to 1990, worldwide harvesting capacity in commercial fisheries grew eight times faster than landings (Gréboval and Munro 1999), and overcapacity has been a significant contributor to the overexploitation of fisheries (FAO 1997). Continued effort expansion under input controls also obliges regulators to implement further operational constraints, such as shorter fishing seasons, in attempts to ensure that TACs are not exceeded. These constraints often aggravate the race to fish and contribute to further overcapacity (Clark 1982), as occurred in the BC halibut fishery before the implementation of individual harvesting rights, as well as in numerous other fisheries. The resulting capacity overhang makes fisheries less robust to management errors, especially in setting appropriate TACs, and also creates political pressures by fishers to increase the total harvest.

When overcapacity reaches a critical level, regulators frequently resort to buybacks of vessels or associated fishing licences. Often, the direct costs of buybacks are borne by the public purse and not by the fishers themselves. Buybacks are only a short-term solution to the underlying incentive problem; if they are successful in temporarily increasing the returns to harvesters who continue to fish, higher profits would encourage further investments and effort creep (Weninger and McConnell 2000) and, if anticipated by fishers, may even detract from conservation efforts (Clark et al. 2005). As a result, the ability of buybacks to reduce long-term fishing effort and help stocks recover is limited (Holland et al. 1999) without a corresponding change in fisher incentives (Fox et al. 2003*b*). For example, buybacks initiated in the northeast groundfish fishery in the United States reduced the number of permits and the number of vessels employed but do not appear to have resulted in observable conservation benefits (Walden et al. 2003). In the BC salmon fishery, there have been five buybacks at a cumulative cost of several hundred million dollars over the period 1970–2000. Although these buybacks may have temporarily reduced the severity of the overcapacity problem caused by both effort creep and a decline in the size of some salmon runs, they have not provided a lasting solution to the chronic problem of overcapacity (Schwindt et al. 2003; Grafton and Nelson 2005).

Transferability, costs, returns, and subsidies

Transferable harvesting rights, and the prices that they can command, induce some fishers to exit and remove excess fishing capacity, thereby increasing returns to the fishers who remain. For transfers of rights to function efficiently, the market for harvesting rights must be competitive and prices must convey useful information about the profitability and status of fish stocks. A recent study of New Zealand's markets for individual harvesting rights, the most comprehensive of any fisheries jurisdiction, found that prices there do reflect ecological variability and changes in fishing profitability (Newell et al. 2005).

High values for harvesting rights, concentration of these rights, or simply the gratis allocation of harvesting rights over a public resource are viewed by some as inequitable (Walters and Martell 2004), especially if the initial allocation of rights excludes crew members and traditional participants in the fishery. To address some of these concerns, it is possible to limit the amount of harvesting rights owned by any one individual or company, or to even set aside a share of the rights as a code-of-conduct quota to promote the interest of the crew, as has occurred in the BC groundfish trawl fishery (Rice 2003). A share of the increased returns (and long-term value of rights) attributable to incentive-based approaches may also be captured to reduce the entry costs for prospective fishers and to collect revenues for the public purse (Grafton 1995).

Individualized and exclusive rights not only identify resource users and limit their number, but also limit the specific magnitude of the interests of each individual fisher in terms of the TAC. This allows research and management costs attributable to fishing activity to be charged proportionally to the beneficiaries. Such cost recovery introduces a new and pow-

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erful dynamic into the relationship between fishers and regulators that has potential to drive down management costs, improve voluntary compliance, and encourage collective action and greater fisher participation in management and research.

Higher fisher returns with IAFs allow the possibility of fisher-funded monitoring and additional data collection. Incentive-based approaches also reduce the motivation for price supports or vessel and gear subsidies, which contribute to overfishing (Milazzo 1998; Munro and Sumaila 2002). For example, Iceland and New Zealand both have long-term individual harvesting rights in many of their fisheries and had government financial transfers in the late 1990s equal to about 4% of the total value of their respective landings (see table A.2 in Cox and Schmidt 2002). In contrast, the total government financial transfers to fisheries regulated with input controls are often much higher. In 1999, for instance, total government transfers were, on average, some 20% of the total value of landings in OECD (Organization for Economic Cooperation and Development) countries (see table A.4 in Cox and Schmidt 2002).

Because traditional input regulation contributes to overcapacity and low fishing incomes, it stimulates government financial transfers. In contrast, IAFs may be viewed as generating a win–win situation: better sustainability outcomes at a lower overall cost of management (including transfers). Indeed, a recent comparison of Iceland, Norway, and Newfoundland showed that the costs of fisheries management, not including government financial transfers, were lowest in Iceland, the country that has gone the furthest to implement secure fishing rights in any of these three jurisdictions (Arnason et al. 2003).

Adjustment costs, economic viability, and flexible decision making

A key concern, especially to crew, is that IAFs reduce employment and create other adjustment costs (OECD 2000). The impact on employment, however, depends on the extent to which the fishery is overexploited in an economic sense. For example, in New Zealand, the total employment and number of vessels actually increased in the first 5 years after the introduction of individual harvesting rights (Davidse et al. 1997; Connor 2001) as a result of the domestication of deep-water fisheries and increased harvests from some relatively unexploited stocks. When harvesting rights reduce employment, as might be expected in fisheries characterized by poor returns and overcapacity, the adjustment costs should be weighed against the possibility of declining returns, ongoing difficulties with traditional input controls, and the probability that current employment levels under existing regulations are unsustainable.

Political decision making, with respect to fisheries management, is influenced by economic circumstances. Where there are many fishers with poor incomes and few alternative employment opportunities, it is much more difficult to reduce current catches to sustainable levels than when fishing is economically viable. In other words, inappropriate incentives that generate low fisher incomes reduce management flexibility and, therefore, increase the likelihood of risk-prone decisions (Sissenwine and Rosenberg 1993). In contrast, incentive approaches promote economic performance. Thus, when an unexpected negative shock arises, the economic impact is less critical and the management response is likely to be quicker and more effective. The incentive approach, therefore, helps to avoid the social and biological amplification of natural fisheries variability, a highly desirable characteristic of fisheries management (Rice 2002).

Sustaining ecosystems

Harvesting, community, and territorial rights do not guarantee that all fishery practices will be sustainable, but they can create incentives for fishers to protect their rights by discouraging practices that are overtly damaging, and promote actions that conserve target species. We address how different incentives can contribute to sustaining ecosystems in the following three subsections.

Multiple stakeholders and collective action

In New Zealand, commercial fishers have recognized that the environment of the Fiordland, listed as a UNESCO World Heritage Site, is vulnerable to harvesting. To address these concerns, an alliance of conservation groups, commercial and recreational fishers, and Maori interests, called the Fiordland Marine Guardians (FMG), developed a strategy to protect environmental quality while providing for sustainable harvesting. It creates eight fully protected marine reserves and several no-anchoring zones, excludes commercial fishing from all inland waters, creates a tailored recreational fishing regime, and establishes the FMG as a formal advisory body to the government (New Zealand Government 2005). Without well-defined harvesting rights and the incentives they engender, this successful balancing of interests and responsibilities across stakeholders would have been impossible.

Coordination and effective oversight

Despite the potential of IAFs to contribute to sustainability, a public oversight and coordination role to integrate commercial resource use with environmental impacts and other resource interests is still required, because it is not possible to specify property rights over every aspect of the environment in advance and thus prevent all the negative spillovers that might arise from harvesting. Public oversight is also needed to manage straddling fish stocks and highly migratory species and for the setting of societal objectives and target and reference points in terms of fish stocks and marine ecosystems. Coordination and oversight may also be justified if the average cost of monitoring and enforcement is lower when there are a greater number of fisheries under surveillance, if the average cost to provide management services is lower with a larger number of services (e.g., science advice, monitoring, and research), or if there is a public-good aspect (such as species diversity) to fisheries management (Grafton 2000).

One of the more important factors in justifying public oversight, in terms of sustainability, is the deleterious impact on the marine environment from fishing that is incidental to the catches of target species (Scott 1999*b*). For example, longlining can cause incidental catch of sea turtles and sea birds, trawling for shrimp can contribute to turtle mortality, and purse seining for tuna can, in some cases, result in inci-

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dental dolphin deaths (Dayton et al. 2002). If reduced numbers of sea birds, turtles, and dolphins do not affect the value of fishers' harvesting rights over target species and reducing these incidental catches is costly, then there is no financial incentive for fishers to address these bycatch issues.

Quantity and price incentives for ecological services

Where threats to ecological services arise and are deemed sufficiently costly by society to warrant intervention, fishers can be given incentives to employ bycatch reduction devices, to make conservation investments, or to undertake practices that may reduce the adverse impacts of fishing. The potential of a quantity-based incentive approach compared with traditional input controls can be illustrated by regulations that are part of the 1998 Agreement on the International Dolphin Conservation Program in the Eastern Tropical Pacific (Hedley 2001). As part of this agreement, vessels flagged by signatory countries that exceed their annual dolphin mortality limits (DMLs) must stop fishing. On all vessels greater than 400 tons (1 ton = 1.016 tonnes), DMLs are enforced by onboard observers who record the numbers of dolphins killed from the harvesting of yellowfin tuna (*Thunnus albacares*). Although these rights are by no means complete property rights (Campbell et al. 2000*b*), some reassignment of unused or forfeited rights is permitted, and in the first year of their introduction, DMLs helped to reduce total dolphin mortality by more than 75% (Hedley 2001).

Habitat damage can arise from some forms of harvesting, such as bottom trawling (Jennings and Kaiser 1998; Dayton et al. 2002; ICES 2005*b*). This could potentially be mitigated through incentives, e.g., through the use of transferable habitat impact units (HIUs) that would proxy marginal habitat damage associated with different gear and habitats (Holland and Schnier 2004). The total number of HIUs would be set to ensure a desired level of habitat protection and would be enforced with a vessel monitoring system that would track each vessel's location and rate of movement. Fishers would be motivated to take into account the impact of fishing on habitats because HIUs would be scarce and tradable. Those who exceed their initial allocation of HIUs would be required to purchase more units, which would increase their fishing costs, whereas those who have HIUs left over after fishing could sell or lease them to others at a profit.

A price-based approach to sustaining ecosystems could involve the imposition of environmental charges on vessels that impose a particular risk or harm to the marine environment and then the use of the funds from these charges to undertake conservation investments. For example, an industry association of gillnet fishers in California have proposed a turtle tax, related to turtle mortality from swordfish (*Xiphias gladius*) harvesting, to pay for the protection of critical leatherback (*Dermochelys coriacea*) nesting sites in Agua Blanca, Baja California (C. Janisse, Federation of Independent Seafood Harvesters (FISH), P.O. Box 352, Bridgewater Corners, VA 05035, USA, cjanisse@vermontel.net, unpublished data). Similar approaches could also be adopted in other fisheries, especially if public, private sector, or nongovernmental funds were used to provide financial incentives for fishers to undertake more sustainable fishing practices. These could, for example, include the eco-certification of sustainable fisheries (Peterman 2002) and harvesting practices to provide a price premium for ecology-friendly fishing, vessel- or gear-specific harvesting charges to promote sustainable practices, and market-based instruments to price ecosystem services. A price-based approach that would help maximize the environmental payoff per dollar of conservation expenditures by regulators or nongovernmental organizations would be to allow fishers to bid or tender for biodiversity conservation payments to undertake specific management actions, but within a framework of well-defined ecological quality objectives (ICES 2005*b*, pp. 32–60). Such an approach has proved successful in changing practices by landholders and has promoted conservation in a cost-effective manner on farms in the State of Victoria, Australia (Stoneham et al. 2003).

Both price- and quantity-based incentives complement ecosystem approaches because they reduce the negative effects of harvesting on endangered and protected species and help to conserve nonmarketed ecosystem services. The key insight from experience to date in commercial fisheries is that appropriate fisher incentives, coupled with public research, monitoring, and effective oversight, promote more sustainable fishing practices.

Concluding remarks

The alarming trends in the world's fisheries demand a fundamental change in management and fishing practices. As managers grapple with these problems, many scientists are arguing for a new paradigm and, in particular, an ecosystem approach to fisheries to overcome the failures of single- or target-species management. While the ecosystem approach and existing strategies that promote sustainability are necessary, especially to account for fishery–ecosystem interactions, they are insufficient by themselves to address the key drivers of unsustainable outcomes, i.e., inappropriate incentives for fishers and the ineffective governance that exists in commercial fisheries regulated exclusively by input controls and TACs. Evidence from more than a dozen natural experiments of commercial, developed fisheries supports our conclusion: incentive-based approaches that better specify individual and group harvesting rights and (or) territorial rights, as well as price ecosystem services, promote both economic and ecological sustainability.

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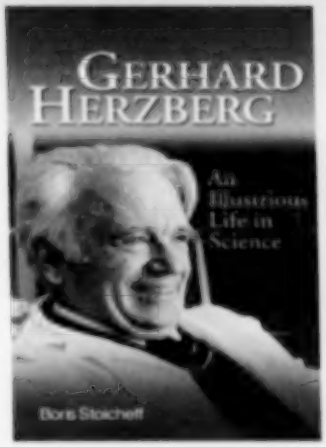

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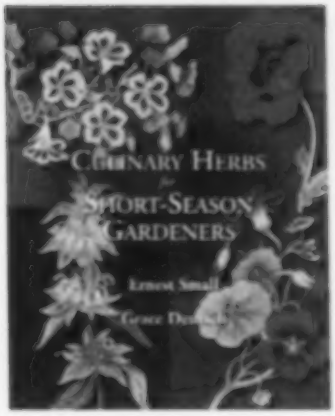

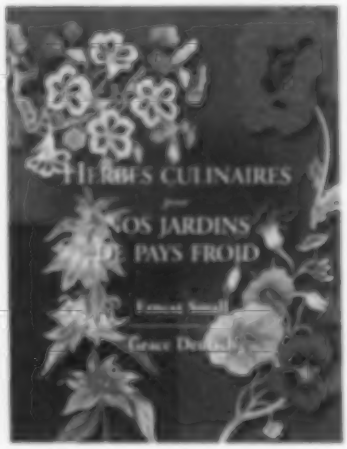

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